

QL  
401  
N314  
INVZ

# HE NAUTILUS

Volume 134, Numbers 3-4  
December 18, 2020  
ISSN 0028-1344

A quarterly devoted  
to malacology.



**EDITOR-IN-CHIEF****José H. Leal**

The Bailey-Matthews National  
Shell Museum  
3075 Sanibel-Captiva Road  
Sanibel, FL 33957 USA

**EDITOR EMERITUS****M. G. Harasewych**

Department of Invertebrate Zoology  
National Museum of  
Natural History  
Smithsonian Institution  
Washington, DC 20560 USA

**CONSULTING EDITORS****Rüdiger Bieler**

Department of Invertebrates  
Field Museum of  
Natural History  
Chicago, IL 60605 USA

**Arthur E. Bogan**

North Carolina State Museum of  
Natural Sciences  
Raleigh, NC 27626 USA

**Philippe Bouchet**

Laboratoire de Biologie des  
Invertébrés Marins et Malacologie  
Muséum National d'Histoire  
Naturelle  
55, rue Buffon  
Paris, 75005 FRANCE

**Robert H. Cowie**

Center for Conservation Research  
and Training  
University of Hawaii  
3050 Maile Way, Gilmore 409  
Honolulu, HI 96822 USA

**Kenneth A. Hayes**

Bernice Pauahi Bishop Museum  
Honolulu, HI 96817

**Steffen Kiel**

Department of Paleobiology  
Swedish Museum of Natural History  
Box 50007  
104 05 Stockholm, SWEDEN

**Harry G. Lee**

4132 Ortega Forest Drive  
Jacksonville, FL 32210 USA

**Charles Lydeard**

Biodiversity and Systematics  
Department of Biological Sciences  
University of Alabama  
Tuscaloosa, AL 35487 USA

**Bruce A. Marshall**

Museum of New Zealand  
Te Papa Tongarewa  
P.O. Box 467  
Wellington, NEW ZEALAND

**Paula M. Mikkelsen**

Paleontological Research  
Institution  
1259 Trumansburg Road  
Ithaca, NY 14850 USA

**Diarmaid Ó Foighil**

Museum of Zoology and Department  
of Biology  
University of Michigan  
Ann Arbor, MI 48109-1079 USA

**Gustav Paulay**

Florida Museum of Natural History  
University of Florida  
Gainesville, FL 32611-2035 USA

**Gary Rosenberg**

Department of Mollusks  
The Academy of Natural Sciences  
1900 Benjamin Franklin Parkway  
Philadelphia, PA 19103 USA

**Elizabeth Shea**

Mollusk Department  
Delaware Museum of  
Natural History  
Wilmington, DE 19807 USA

**Ángel Valdés**

Department of Malacology  
Natural History Museum  
of Los Angeles County  
900 Exposition Boulevard  
Los Angeles, CA 90007 USA

**Geerat J. Vermeij**

Department of Geology  
University of California at Davis  
Davis, CA 95616 USA

**SUBSCRIPTION INFORMATION**

The subscription rate for volume 135 (2021) is US \$65.00 for individuals, US \$102.00 for institutions. Postage outside the United States is an additional US \$10.00 for regular mail and US \$28.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

*Change of address:* Please inform the publisher of your new address at least 6 weeks in advance. All communications should include both old and new addresses (with zip codes) and state the effective date.

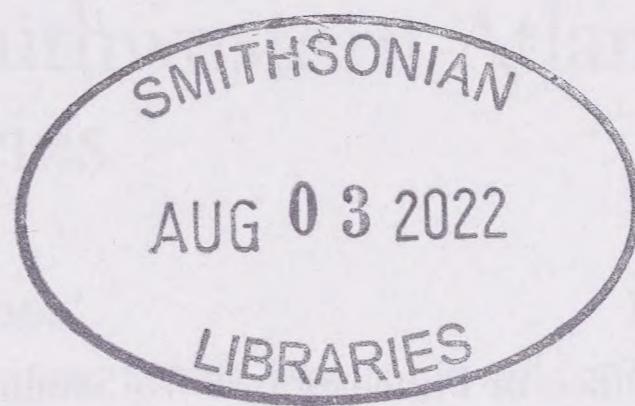
THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews National Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS  
P.O. Box 1580  
Sanibel, FL 33957

# THE CONAUTILUS

## CONTENTS



Volume 134, Number 3-4

December 18, 2020

ISSN 0028-1344

<b>Leonardo S. Souza</b>	A new species of <i>Tritonoharpa</i> Dall, 1908 (Gastropoda: Cancellariidae) from the southwestern Atlantic and an overview of other western Atlantic species .....	95
<b>Renata S. Gomes</b>		
<b>Paulo Márcio S. Costa</b>		
<b>Charles L. Powell, II</b>	Memorial to Warren O. Addicott—A remarkable student of Tertiary marine	
<b>Kevin J. Meade</b>	mollusks of the northeastern Pacific .....	107
<b>Shawn G. Wiedrick</b>		
<b>Roland Houart</b>	Six new species of <i>Paciocenebrina</i> (Gastropoda: Muricidae: Ocenebrinae) from the northeast Pacific .....	117
<b>Kazutaka Amano</b>		
<b>Hiroshi Kurita</b>	A new species of <i>Arca</i> (Bivalvia: Arcidae) from the lower Miocene Asahi Formation on the Japan Sea side of central Honshu, with remarks on the westward faunal migration from the eastern Pacific .....	132
<hr/>		
<b>RESEARCH NOTE</b>		
<b>Justin N. Voss</b>		
<b>Gabriel A. Delgado</b>	Imposex in the city: First evidence of female masculinization in Queen	
<b>Nancy J. Brown-Peterson</b>	Conch <i>Aliger gigas</i> (Linnaeus, 1758) (Gastropoda: Strombidae) in Florida ....	138
<b>Author Index</b> .....		143

## STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

1. Publication Title, THE NAUTILUS.
2. Publication No. 0028-1344.
3. Filing Date, November 20, 2020.
4. Issue Frequency, Quarterly.
5. No. of Issues Published Annually, Four.
6. Annual Subscription Price, US \$102.00.
7. Complete Mailing Address of Known Office of Publication, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA
8. Complete Mailing Address of Headquarters, same as 7.
9. Full Names and Complete Mailing Addresses of Publisher, The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA  
Editor, Dr. José H. Leal, address as above.
10. Owner, Shell Museum and Educational Foundation, Inc., address as above.
11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities, None.
12. The purpose, function, and nonprofit status of this organization and the tax-exempt status for federal income tax purposes has not changed during the preceding 12 months.
13. Publication Name, THE NAUTILUS.
14. Issue Date for Circulation Data Below, August 4, 2020

	Average 12 months	Single Issue
<b>15. Extent and Nature of Circulation</b>		
a. Total Number of Copies	220	220
b. Paid Circulation		
1. Paid/Requested Outside-County Mail Subscriptions	205	204
2. Paid In-County Subscriptions	0	0
3. Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution	0	0
4. Other Classes Mailed Through the USPS	5	3
c. Total Paid and/or Requested Circulation	210	207
d. Free Distribution by Mail		
1. Outside-County	11	11
2. In-County	0	0
3. Other Classes Mailed Through the USPS	0	0
4. Free distribution outside the Mail	0	0
e. Total Free or Nominal Rate Distribution	6	6
f. Total Distribution	216	213
g. Copies not Distributed	4	3
h. Total	220	216
i. Percent Paid Total	97%	96%
<b>16. Electronic Copy Circulation</b>		
a. Paid Electronic Copies	0	0
b. Total Paid Print Copies + Paid Electronic Copies	210	207
c. Total Print Distribution + Paid Electronic Copies	216	213
d. Percent Paid (Both Print & Electronic Copies)	97%	97%

# A new species of *Tritonoharpa* Dall, 1908 (Gastropoda: Cancellariidae) from the southwestern Atlantic and an overview of other western Atlantic species

**Leonardo S. Souza**

Malacologia, Departamento de Invertebrados  
Museu Nacional, Rio de Janeiro,  
BRAZIL  
leosouza2301@gmail.com

**Renata S. Gomes**

Instituto Mar Adentro, Rio de Janeiro, Brazil  
and  
Malacologia, Departamento de Invertebrados  
Museu Nacional, Rio de Janeiro, BRAZIL

**Paulo Márcio S. Costa**

Fundação Instituto de Pesca do Estado do Rio de Janeiro  
Escritório Regional Costa Verde, Angra dos Reis, Brazil  
and  
Malacologia, Departamento de Invertebrados  
Museu Nacional, Rio de Janeiro, BRAZIL

## ABSTRACT

A new southwestern Atlantic species belonging to genus *Tritonoharpa* is described from northeastern and southeastern Brazil. ***Tritonoharpa curvapex* new species** has a strongly deviated nucleus in the protoconch, which is the main feature that distinguishes it from the remaining congeners from the western Atlantic. Shell dimensions and number of cords in the teleoconch also distinguish this new species from the other *Tritonoharpa*. An overview of the remaining extant *Tritonoharpa* from the western Atlantic is also presented. We provide taxonomical remarks, illustrations and the known distribution of *Tritonoharpa lanceolata* (Menke, 1828), *Tritonoharpa cubapatriae* (Sarasúa, 1975), *Tritonoharpa bayeri* (Petuch, 1987), *Tritonoharpa leali* Harasewych, Petit, and Verhecken, 1992 and *Tritonoharpa janowskyi* Petuch and Sargent, 2011.

*Additional Keywords:* Neogastropoda, Volutoidea, Plesiotritoninae, taxonomy

1992 and *T. janowskyi* Petuch and Sargent, 2011. *Tritonoharpa lanceolata* is currently known from several localities in the western Atlantic, occurring from the eastern USA to southeastern Brazil (Beu and Maxwell, 1987; Rios, 2009). *Tritonoharpa cubapatriae* is known from Cuba and Panama (Caribbean coast) (Sarasúa, 1975; Lee, 2009). *Tritonoharpa bayeri* and *T. janowskyi* are known only from their type localities off Caribbean Colombia and Florida, USA, respectively. *Tritonoharpa leali* is currently restricted to the states of Bahia, Espírito Santo, and Rio de Janeiro, Brazil (Harasewych et al., 1992; Absalão et al., 2006). Thus, until now *T. lanceolata* and *T. leali* are the only species recorded in Brazil (Harasewych et al., 1992; Absalão et al., 2006; Rios, 2009).

Verhecken (1991) commented on the scarcity of records or descriptions of Cancellariidae in the western Atlantic south of the Equator, but since then reports on cancellariids from Brazil increased considerably, especially in deep-sea studies (Harasewych et al., 1992; Simone and Birman, 2006; Barros and Lima, 2007; Barros and Petit, 2007; Lima et al., 2007). Recent surveys of malacological collections in Brazil revealed an undescribed species of *Tritonoharpa* from the coast of Brazil and the need for a revision of other known congeners in the western Atlantic. We formally describe ***Tritonoharpa curvapex* new species** and provide taxonomical comments on the other western Atlantic *Tritonoharpa*.

## INTRODUCTION

The family Cancellariidae Forbes and Hanley, 1851 consists of marine gastropods and is known from all oceans (Lima et al., 2007), but the majority of the species are tropical or temperate (Harasewych and Petit, 2011). This family currently comprises about 350 extant species (MolluscaBase, 2020) and presents a great variety of shell features (Modica et al., 2011b). Most recent classifications include three subfamilies: Cancellariinae Forbes and Hanley, 1851, Admetinae Troschel, 1865 and Plesiotritoninae Beu and Maxwell, 1987 (Modica et al., 2011b; Bouchet et al., 2017).

Among the Plesiotritoninae, the genus *Tritonoharpa* Dall, 1908 is one of the most diverse with 19 extant valid species (MolluscaBase, 2018). Five species of *Tritonoharpa* are known from the western Atlantic: *T. lanceolata* (Menke, 1828), *T. cubapatriae* (Sarasúa, 1975), *T. bayeri* (Petuch, 1987), *T. leali* Harasewych, Petit and Verhecken,

## MATERIALS AND METHODS

The material studied consists mostly of empty shells deposited in malacological collections, collected by various oceanographic expeditions and smaller collecting events. The largest expeditions are: 1. REVIZEE Central: “Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva, Score Central” (Program of Evaluation of the Sustainable

Potential of Living Resources in the Economic Exclusive Zone), carried out by “Ministério do Meio Ambiente”, Brazilian government, samples collected by the research vessel (R/V) ANTARES and the supply-boat ASTRO GAROUPA between 1996–2002; 2. BPOT MR: “Projeto de Caracterização e Monitoramento Ambiental da Bacia Potiguar – Malha Regional” (Project of Environmental Characterization and Monitoring of Potiguar Basin – Regional Grid), carried out by Petrobras SA, samples collected by the supply-boat ASTRO GAROUPA between 2002–2004; 3. AMBES: “Caracterização Ambiental Marinha da Bacia do Espírito Santo e porção Norte da Bacia de Campos” (Marine environmental characterization of the Espírito Santo Basin and North part of Campos Basin), carried out by Petrobras SA, samples collected by the R/V LUKE THOMAS and R/V SEWARD JOHNSON, between 2010–2013.

Most shells were photographed (using focus stacking) by an AxioCam ICc 5 camera coupled to a stereomicroscope ZEISS Discovery.V20. A few shells were studied under a scanning electron microscope (SEM) Jeol JSM-6390LV for a detailed examination of sculpture. Shell measurements are: shell length (SL), body whorl length (BWL), aperture length (AL), shell width (SW), aperture width (AW), protoconch height (PCH) and width (PCW). The counting of protoconch whorls follows Verduin (1982) and Verhecken (2007). Some shells were treated with mineral oil to enhance the color pattern.

Collection acronyms are: ANSP: Academy of Natural Sciences of Philadelphia, Drexel University, Philadelphia; FLMNH: Florida Museum of Natural History, Gainesville; IBUFRJ: Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MORG: Museu Oceanográfico “Professor Eliézer de Carvalho Rios”, Universidade Federal do Rio Grande, Rio Grande, Brazil; MZSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; SMF: Naturmuseum Senckenberg, Frankfurt, Germany; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

Due to the recent fire at the Museu Nacional in Brazil (Zamudio et al., 2018) most lots from this institution listed in the material examined here, in addition to lots lent from other institutions, were destroyed. Destroyed specimens (spm) or shells (sh) are marked by a dagger (†) in the material examined of each species.

## SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851  
Subfamily Plesiotritoninae Beu and Maxwell, 1987

### Genus *Tritonoharpa* Dall, 1908

*Nivitriton* Iredale, 1929. Type species: *Triton antiquatus* Hinds in Reeve, 1844 (by original designation); Recent, tropical Indo-Pacific.  
*Esbeta* Sarasúa, 1975. Type species: *Ranella lanceolata* Menke, 1828 (by original designation); Miocene to Recent, western Atlantic.

**Type Species:** *Tritonoharpa vexillata* Dall, 1908 (by original designation); Recent, western America and the Galapagos Island.

**Description:** Shell with weakly to moderately convex teleoconch whorls, retaining prominent varices on early as well as later whorls, well developed columellar collar, lacking columellar plaits or with a single very low, narrow columellar plait, and with a nematoglossan radula, consisting of a thin membrane and one central row of rachidian teeth (adapted from Beu and Maxwell, 1987 and Modica et al., 2009).

### *Tritonoharpa curvapex* new species (Figures 1–9)

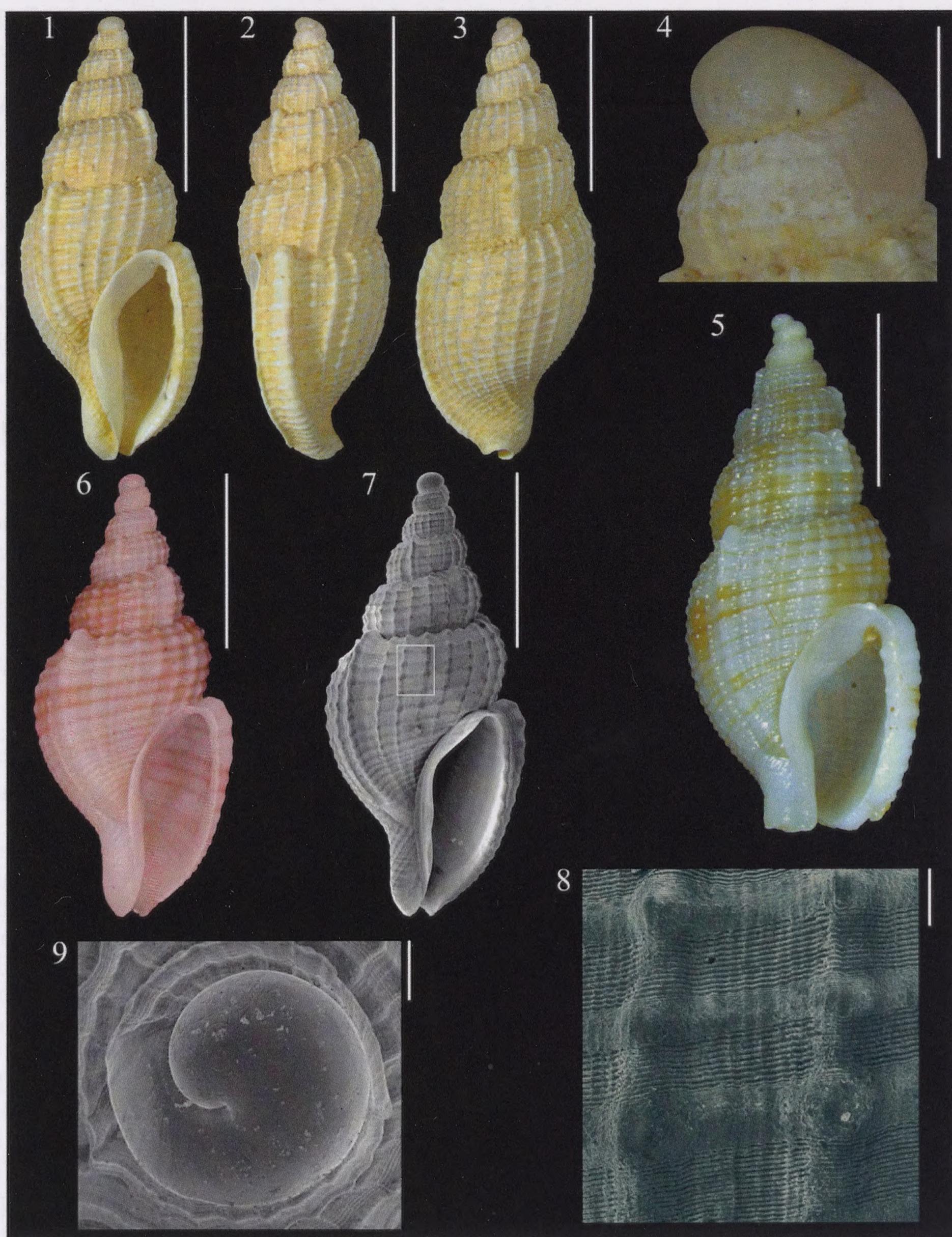
**Diagnosis:** Shell up to 15.0 mm long, 5.5 mm wide, with 6–7 whorls, cream to light brown, with scattered brown blotches and thin spiral bands. Whorls convex, with moderately prominent varices (1–2 per whorl) from early whorls to later whorls, sculptured with cancellate pattern. Protoconch paucispiral, smooth, 1.0 whorl, nucleus strongly deviated.

**Description:** Shell about 15.0 mm long, 6.5 mm wide, spire angle 35°, shouldered. Protoconch paucispiral, 1.0 whorl, nucleus deviated about 30° from teleoconch axis. Protoconch–teleoconch transition abrupt, marked by a thin lip and onset of cancellate sculpture. Teleoconch with up to 7 whorls, moderately inflated, weakly shouldered; suture deeply impressed, almost obscured by the axial coronation of succeeding whorl. Spiral and axial cords present, producing cancellate sculpture; strong nodules at the intersection of spiral and axial cords; spiral cords more pronounced than axial cords. Varices high, non-collabral, narrow, appearing periodically in every 2/3 whorl. About 11 axial ribs between varices in the last whorl; About 16 spiral cords from the suture to the beginning of the siphonal canal in the last whorl (frontal view). Aperture wide, elliptical, with well-defined posterior notch. Inner lip smooth, with columellar collar reflected over, but not adherent to, fasciole and pseudoumbilicus. Outer lip with up to 8 pairs of denticles confined to flared region beyond varix. Siphonal canal short, weakly deviated, partially covered abaxially. Shell color cream to brownish, with scattered brownish blotches and thin spiral bands.

**Type Locality:** Brazil: Northeast coast, imprecise locality between Pernambuco and Bahia states, coll. 1977.

**Type Material: Holotype:** IBUFRJ 5430 (sh). **Paratypes:** Brazil: Bahia state: Camamu Basin, 13°28'29" S 38°48'41" W, 30 m (MNRJ 14925, 1 sh†; MNRJ 27973, 1 sh†); Espírito Santo state: REVIZEE Central I stn. C65, 18°52'58" S 39°06'00" W, 50 m, coll. R/V Antares, 25/iv/1996 (IBUFRJ 9525, 1 sh).

**Measurements:** Holotype, IBUFRJ 5430: Whorls= 6.0; SL= 12.7 mm; BWL= 8.5 mm; AL= 6.0 mm; SW= 5.2 mm; AW= 2.7 mm; PCH= 0.8 mm; PCW= 0.9 mm; SL/SW= 2.4.



**Figures 1–9.** *Tritonoharpa curvapex* new species. **1–4.** Holotype, IBUFRJ 5430. **5.** Paratype, MNRJ 27973. **6–9.** Paratype, MNRJ 14925. **1, 5–7.** Entire shell in frontal view, white square in 7 indicates detail in 8. **2.** Entire shell in lateral view. **3.** Entire shell in dorsal view. **4, 9.** Detail of protoconch, lateral and apical views, respectively. **8.** Detail of teleoconch surface. Scale bars: **1–3, 5–7** = 5 mm; **4** = 500  $\mu$ m; **8–9** = 200  $\mu$ m.

**Etymology:** *Curvus*, Latin for bent; *apex*, Latin for tip; referring to the strongly deviated nucleus of the protoconch.

**Distribution:** Brazil: From Pernambuco to Espírito Santo. Empty shells from depths between 30 m to 50 m.

**Remarks:** The holotype IBUFRJ 5430 (Figures 1–4) and the paratype IBUFRJ 9525 of *T. curvapex* are safely preserved in the IBUFRJ collection. The other paratypes (Figures 6–9) were destroyed by the fire. To avoid the

designation of a destroyed specimen as the holotype, the shell of IBUFRJ 5430 was selected as the holotype despite the imprecise locality of collection.

*Tritonoharpa curvapex* differs from all other western Atlantic species of the genus in having a conspicuous protoconch in which the nucleus is strongly deviated (Figures 4, 9). This newly described species is most similar to *T. bayeri* (Figures 23–27) based on the general shape and on having an aperture that is not very constricted posteriorly. The protoconch of the holotype of *T. bayeri* (USNM

859853) is partially broken (Figures 25, 26), but it is possible to note that the nucleus is not deviated as in *T. curvapex*. *Tritonoharpa curvapex* can also be distinguished from *T. bayeri* by the relatively smaller dimensions of the shell (12.7 mm long, 5.2 mm wide vs. 16.2 mm long, 7.6 mm wide, respectively, both with 5 whorls) and by the smaller number of axial ribs between varices of the last whorl (11 vs. 16-18). These species also differ by their color pattern, *T. curvapex* has brownish spots like *T. bayeri*, but also some spiral bands (Figure 5) that are not present in *T. bayeri*.

*Tritonoharpa curvapex* also resembles *Tritonoharpa ponderi* Beu and Maxwell, 1987, from Australia, and *Tritonoharpa caunbonensis* Pacaud, Ledon, and Loubry, 2015, an extinct species from the Eocene of Paris Basin, because these species also have a strongly deviated protoconch (Beu and Maxwell, 1987: pl. 18, fig. E, I; Pacaud et al., 2015: pl. 10, fig. 1E). However, *T. curvapex* can be distinguished from *T. ponderi* by the abrupt increase in diameter of the teleoconch, which occurs more gradually in *T. ponderi*. *Tritonoharpa curvapex* can be distinguished from *T. caunbonensis* by its relatively larger size (holotype of *T. curvapex*, IBUFRJ 5430, ~6 whorls, 12.7 mm long, 5.2 mm wide, SL/SW = 2.4 vs. holotype of *T. caunbonensis*, MNHN.F.A51472, ~7 whorls, 10 mm long, 3.9 mm wide, SL/SW = 2.6), and in having thinner varices and a narrower inner lip.

#### Notes on Other Western Atlantic *Tritonoharpa*

##### *Tritonoharpa lanceolata* (Menke, 1828)

(Figures 10-20)

*Ranella lanceolata* Menke, 1828: 87.

For synonymy up to 1987, see Beu and Maxwell (1987: 40) *Colubraria lanceolata* (Menke, 1828) – Perry and Schwengel (1955: 158, pl. 31, fig. 222); Daccarett and Bossio (2011: 94, fig. 444).

*Tritonoharpa lanceolata* (Menke, 1828) – Lyons (1989: 26, pl. 9, fig. 1); Lyons (1998: 27 [annotated list]); Petit and Harasewych (2005: 63 [annotated list]); Wolfe (2008 [annotated list]); Tunnell Jr. et al. (2010: 234); Espinosa et al. (2012: 291, fig. 525); Lamy and Pointier (2017: 528, pl. 184, fig. 9A-B).

**Type Locality:** Puerto Rico (Menke, 1828).

**Type Material:** Probably lost. After K.T. Menke's death his collection was sold and dispersed (Zilch, 1967; Kohn, 1988). The most probable place to find would be the SMF, however there is no material that seems to belong to Menke's material of *T. lanceolata* (Sigrid Hof, pers. comm.).

**Other Material Examined:** USA: Georgia: off Georgia (30°54'18" N, 80°36'06" W, 34 m), coll. R/V BAGBY, 26/iii/1980: USNM 824010 [3 sh]; Florida: 12 miles Northeast Cape Canaveral (28°37' N, 80°30' W): USNM 486176 [1 sh]; Oculina Reef (27°50' N, 79°58' W, 91 m), coll. Houbrick: USNM 798073 [1 sh]; W of Boca Grande (26°44' N, 84°09' W, 55 m), coll. 1971: ANSP 395042 [6

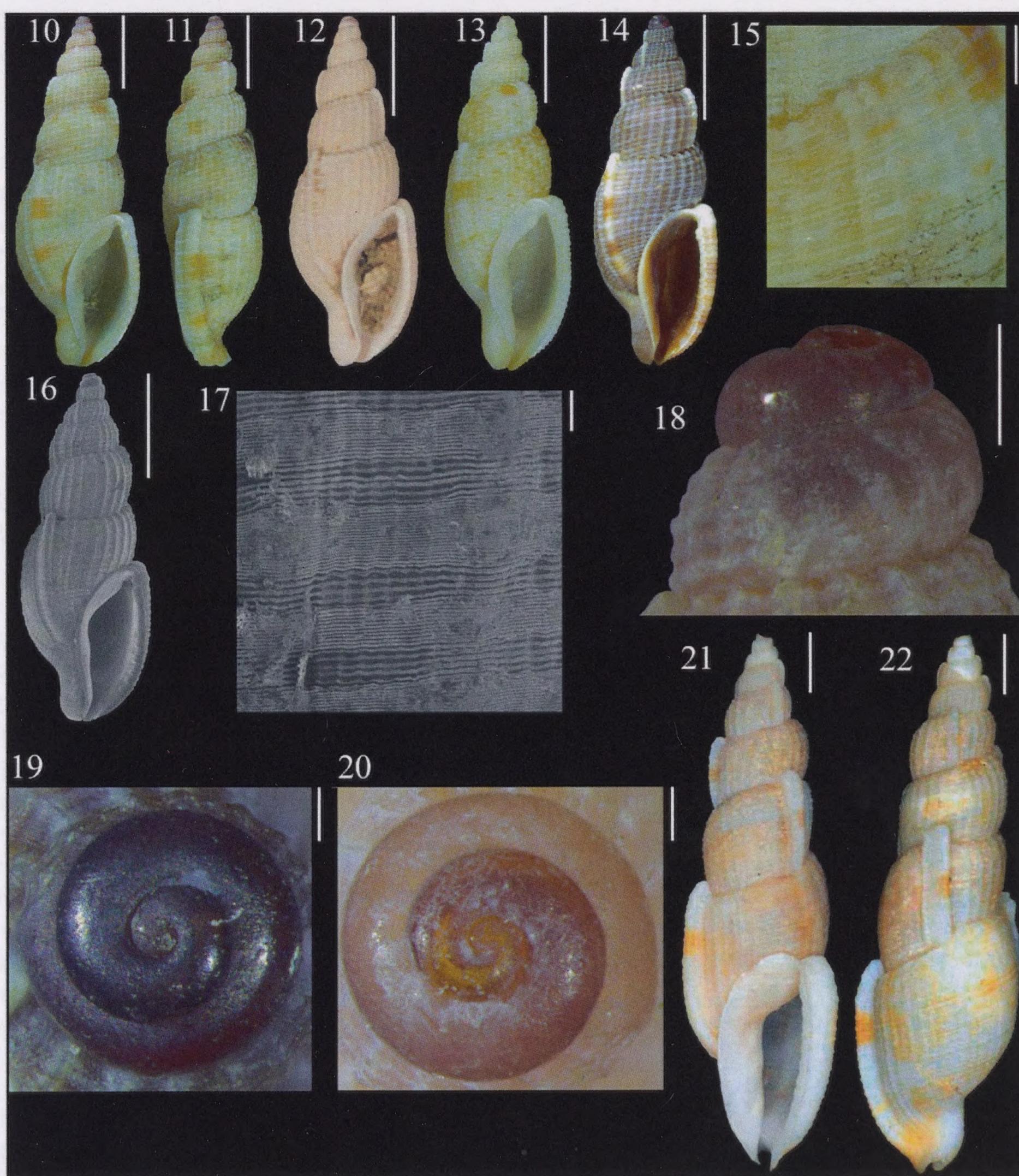
sh]; Off Key West (182-213 m), coll. IX/1963: ANSP 294763 [1 sh]. Caribbean area: Jamaica: Montego Bay, coll. A. L. Mhering, 17/xii/1954: USNM 712137 [1 sh]. Panama: Minas Bay, Payardi Island: USNM 743644 [2 sh]. Haiti: Jeremy: USNM 383239 [1 sh]. Dominican Republic: Las Galeras, Samaná Bay (2 m), coll. 1994: ANSP 408384 [2 sh]. Puerto Rico: North of Mayaguez Docks: USNM 662026 [2 sh]. Virgin Islands: St. Thomas, coll. Brady, 1968: USNM 702792 [2 sh]. Anguilla: Sombrero Island: USNM 92993 [1 sh]. Grenada: Grand Anse Bay (12°01'46" N, 61°46'19" W, 3-6 m), coll. 08/x/2012: MZSP 108664 [1 sh]. Trinidad and Tobago: Off Scarborough, coll. 30/xi/1989: FLMNH 281379 [7 sh†].

**Measurements:** USNM 92993: Whorls = 8.0; ANSP 395042: SL = 29.1 mm; BWL = 17.0 mm; AL = 11.5 mm; SW = 9.0 mm; AW = 6.0 mm; PCH = not measured; PCW = not measured; SL/SW = 3.2. Whorls = 7.5; SL = 24.1 mm; BWL = 14.3 mm; AL = 10.1 mm; SW = 8.6 mm; AW = 4.8 mm; PCH = 1.1 mm; PCW = 1.2 mm; SL/SW = 2.8. ANSP 294763: Whorls = 7.0; SL = 20.2 mm; BWL = 13.7 mm; AL = 9.7 mm; SW = 7.0 mm; AW = 4.4 mm; PCH = 0.8 mm; PCW = 1.0 mm; SL/SW = 2.9.

**Distribution:** USA: New Jersey, North Carolina, Georgia, Florida (Beu and Maxwell 1987), Texas (Rosenberg et al., 2009; Tunnell Jr. et al., 2010). Bermuda (Lamy and Pointier, 2017); Bahamas (Beu and Maxwell, 1987; Redfern, 2013); Cuba; Haiti (Beu and Maxwell, 1987); Mexico (Vokes and Vokes, 1983; Beu and Maxwell, 1987); Jamaica (Beu and Maxwell, 1987); Honduras (Lamy and Pointier, 2017); Costa Rica (Lamy and Pointier, 2017); Panama (Lamy and Pointier, 2017); Colombia (Daccarett and Bossio, 2011); Puerto Rico (Menke, 1828); Virgin Islands (Mörch, 1877; Beu and Maxwell, 1987); St. Martin (Lamy and Pointier, 2017); Anguilla (Lamy and Pointier, 2017); Guadeloupe (Mörch, 1877; Lamy and Pointier, 2017); Martinique (Mörch, 1877); Trinidad and Tobago (Beu and Maxwell, 1987); Venezuela (Beu and Maxwell, 1987); Suriname (Altena, 1975); Brazil: from North to Southeast coast (?) (Rios 2009). From 0 to 178 m (Rosenberg et al., 2009).

**Remarks:** The whereabouts of the type material of *T. lanceolata* is unknown and as mentioned above, it is probably lost. The original description is not very informative and the species was not figured by Menke (1828), consequently the true identity of *T. lanceolata* is challenging to assess despite being frequently cited in the literature. We have examined one shell from Puerto Rico, area of the type locality which was not precisely defined, but this specimen is severely worn (Figure 12). We follow here the description of Beu and Maxwell (1987) and Harasewych et al. (1992) to recognize *T. lanceolata*.

*Tritonoharpa lanceolata* usually has slightly distorted teleoconch whorls (Figures 10-14, 16) in comparison to its congeners and reaches a larger size. Beu and Maxwell (1987) described a variation of the teleoconch sculpture in *T. lanceolata*, in which axial and spiral cords vary from narrow to thick, resulting in different degrees of



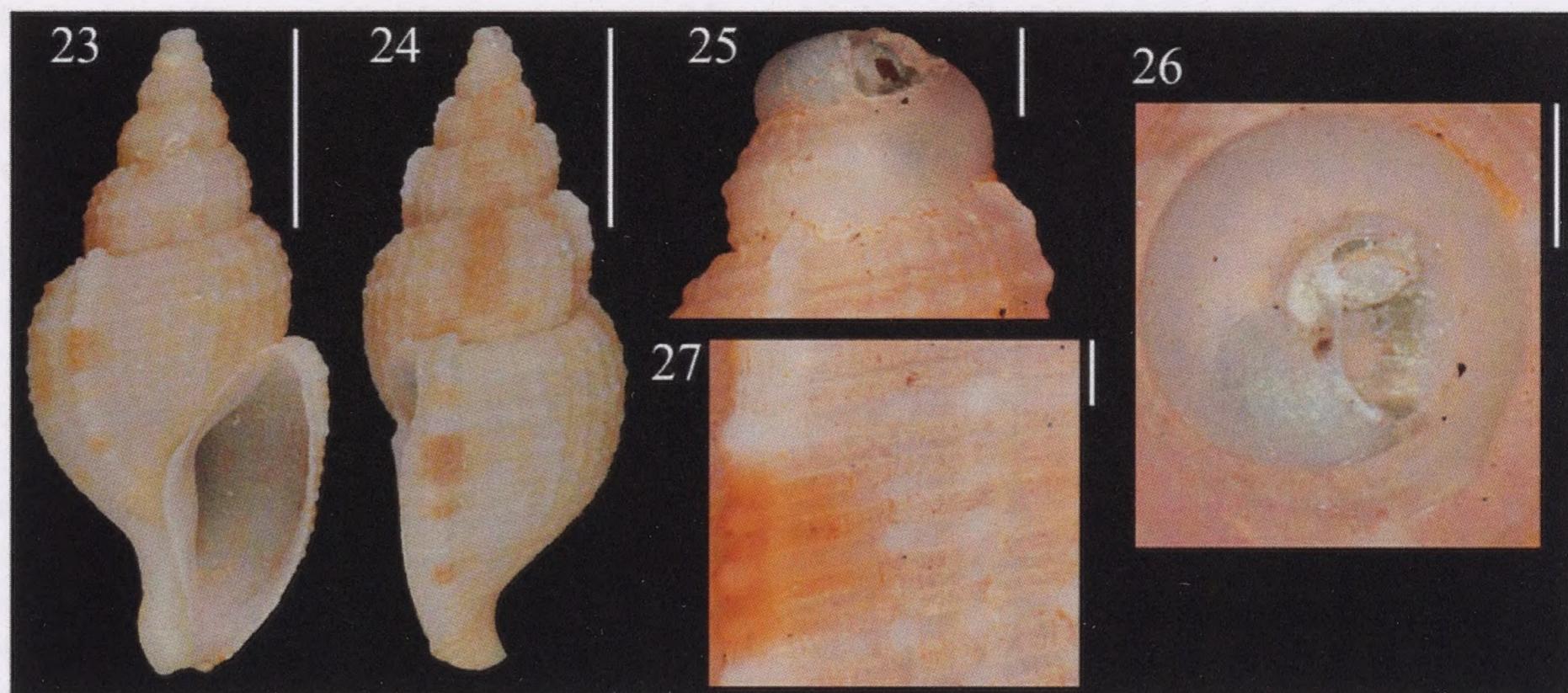
**Figures 10–22.** *Tritonoharpa* species. **10–20.** *Tritonoharpa lanceolata* (Menke, 1828). **10, 11, 18, 20.** ANSP 395042. **12.** USNM 662026. **13, 15.** ANSP 294763. **14, 16, 17, 19.** ANSP 408384. **21, 22.** *Tritonoharpa cubapatriae* (Sarasúa, 1975): holotype, Museo Poey, Universidad de La Habana, Cuba. **10, 12–14, 16, 21.** Entire shell in frontal view. **11.** Entire shell in lateral view. **15, 17.** Detail of teleoconch sculpture. **18.** Detail of protoconch in lateral view. **19, 20.** Detail of protoconch in apical view. **22.** Entire shell in dorsal view. Scale bars: **10–14, 16, 21, 22** = 5 mm; **15** = 1 mm; **17** = 100  $\mu$ m; **18** = 500  $\mu$ m; **19, 20** = 200  $\mu$ m. Credits: **19, 20,** José Espinosa.

nodulation. Harasewych et al. (1992: 45, fig. 8) depicted a detail of the sculpture of *T. lanceolata*, showing spiral cords more pronounced and thicker than axial cords. Shells of *T. lanceolata* examined here also show well developed spiral cords and weaker axial cords (Figure 17).

*Tritonoharpa lanceolata* also has a variable color pattern in the protoconch and teleoconch (Beu and Maxwell, 1987). As currently known, the protoconch varies from pale cream (Figures 12, 13) to purplish (Figures 10, 14, 18–20) and the teleoconch varies from homogeneous pale cream with brownish spots and streaks (Figures 10, 13) to darker shells (Figure 14). Whitish shells are usually beach worn specimens (Figure 12). Until more

evidence about the identity of *T. lanceolata* become available (i.e., discovery of the type material, anatomy, genetics, more material from Puerto Rico), it is difficult to assess if there is more than one distinct species under the same name.

In Brazil, the first record of *T. lanceolata* was reported by Rios (1970) (as “*Colubraria lanceolata*”), who cited localities from the Northeast and Southeast (Trindade Island) regions. Rios (1975; 1985) added a record from the North of Brazil. Later, Rios (1994) recorded *T. lanceolata* only in Pará, North Brazil and Rios (2009) repeated again the records from North to Southeast coast of Brazil. Rios’ illustrations (1975; 1985; 1994;



**Figures 23-27.** *Tritonoharpa bayeri* (Petuch, 1987): holotype of *Colubraria bayeri* Petuch, 1987, USNM 859853. **23.** Entire shell in frontal view. **24.** Entire shell in lateral view. **25, 26.** Detail of protoconch in lateral and apical views, respectively. **27.** Detail of teleoconch sculpture. Scale bars: **23, 24** = 5 mm; **25-27** = 400  $\mu$ m. Credits: **23, 24**, USNM.

2009) do not permit the evaluation of the pattern of sculpture in the teleoconch. Thus, a robust delimitation of the species based on these figures is not possible. Furthermore, despite being a catalogue of mollusks from Brazil, the shells figured by Rios are not always from this country (pers. obs.).

The malacological collections studied in the present work usually housed vouchers from Brazil identified as *T. lanceolata*. However, all the shells from Brazil studied seems to present axial ribs thicker and slightly more pronounced in comparison to the material from the northern hemisphere, but a few shells were studied under SEM. These features lead us to doubt whether *T. lanceolata* does really occur in Brazil.

#### ***Tritonoharpa cubapatriae* (Sarasúa, 1975)** (Figures 21, 22)

*Colubraria (Esbelta) cubapatriae* Sarasúa, 1975: 4, figs. 1-2. *Tritonoharpa cubapatriae* (Sarasúa, 1975) – Petit and Harasewych (1990: 17 [annotated list]; 2005: 42 [annotated list]); Lee (2009: 123); Rosenberg et al. (2009: 661 [annotated list]); Espinosa et al. (2012: 291, fig. 524 [reproduced from original illustration]).

**Type Locality:** Cuba: Habana: Marianao, 20 m.

**Type Material: Holotype:** Museo Poey, Universidad de La Habana, Cuba (sh; here examined). Formerly at “Instituto de Zoología, Academia de Ciencias de Cuba” and catalogued as type number 31 (sh; here examined by photographs) (Sarasúa 1975).

**Distribution:** Cuba (Sarasúa, 1975); Panama (Lee, 2009). Known from 20 m (Sarasúa, 1975).

**Remarks:** Beu and Maxwell (1987: 39) considered this species as the possible largest specimen of *T. lanceolata*

due to the size of the holotype (45 mm long) (Sarasúa, 1975) (Figures 21, 22). According to these authors: “examination of more extremely large western Atlantic specimens will be necessary to be sure of the status of *T. cubapatriae*”. Indeed, the differences pointed by Sarasúa (1975) in comparisons with *T. lanceolata* may be related to the ontogeny phase of the species and we agree with Beu and Maxwell (1987) in that the shell of *T. cubapatriae* does not have more convex whorls than *T. lanceolata*.

The largest specimen of *T. lanceolata* we have examined reaches about eight whorls, 29.1 mm long, collected in Anguilla, Caribbean (USNM 92993). Lamy and Pointier (2017: pl. 184, figs. 9A, B) illustrated a shell from Martinique with 38.4 mm long.

The only additional record of *T. cubapatriae* since its original description was reported by Lee (2009: 123). He referred to material from Caribbean Panama in a private collection, with no information about depth and no illustration.

#### ***Tritonoharpa bayeri* (Petuch, 1987)** (Figures 23-27)

*Colubraria bayeri* Petuch, 1987: 102, pl. 24, figs. 11-12. *Colubraria bayeri* Petuch, 1987 – Daccarett and Bossio (2011: 94, fig. 446).

*Tritonoharpa bayeri* (Petuch, 1987) – Lamy and Pointier (2017: 528, pl. 184, fig. 8A-B).

**Type Locality:** Colombia: Guajira Peninsula, Off Cabo La Vela, 35 m.

**Type Material: Holotype:** USNM 859853 (sh; here examined).

**Measurements:** Holotype, USNM 859853: Whorls= 7.0; SL= 16.2 mm; BWL= 11.5 mm; AL= 8.3 mm; SW= 7.6 mm; AW= 3.7 mm; PCH= 1.0 mm; PCW= 1.2 mm; SL/SW= 2.1.

**Distribution:** Guadeloupe (Lamy and Pointier, 2017), Colombia (Petuch, 1987; Daccarett and Bossio, 2011). From 8 to 35 m (Petuch, 1987; Lamy and Pointier, 2017).

**Remarks:** *Tritonoharpa bayeri* was known only from Colombia until recently when Lamy and Pointier (2017) recorded the species in Guadeloupe. The shell figured by Lamy and Pointier (2017: pl. 184, fig. 8A–B) has a dark brown coloration at the spire, differing from the holotype.

Petuch (1987) introduced the species in *Colubraria* Schumacher, 1817 and made no comparisons to other species of *Tritonoharpa*. *Tritonoharpa bayeri* is very similar to *T. curvapex* and was distinguished above.

*Tritonoharpa bayeri* differs from *T. lanceolata* and *T. leali* by the faster increase in diameter, reaching a smaller ratio of the SL/SW (2.1 vs. 2.8–3.2 and 2.6, respectively). Furthermore, the aperture of *T. bayeri* is not so constricted posteriorly as in *T. lanceolata* and *T. leali*.

*Tritonoharpa bayeri* has a similar ratio of SL/SW to the initial whorls of *T. cubapatriae*, the latter species cease a strong increase in diameter after the fifth or sixth whorl and becomes more cylindrical in shape, reaching a higher number of whorls and length. The presence of thinner and lower varices in *T. bayeri* through all whorls indicates that this species is not a young specimen of *T. cubapatriae*.

### ***Tritonoharpa leali* Harasewych, Petit, and Verhecken, 1992**

(Figures 28–39)

*Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992: 45, figures 1–2, 5–6.

*Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992 – Rios (1994: 155, pl. 51, fig. 683A); Absalão et al. (2006: 244); Rios (2009: 298, fig. 750).

**Type Locality:** Brazil: Vitória-Trindade Seamount Chain, Davis Bank, MD55 stn. DC40, 20°40' S, 34°41' W, 60 m, coll. R/V MARION DUFRESNE, v/1987.

**Type Material: Holotype:** MORG 28659 (sh; here examined). **Paratype:** Brazil: Bahia state: off Itaparica Island (USNM 860521, 1 sh; here examined).

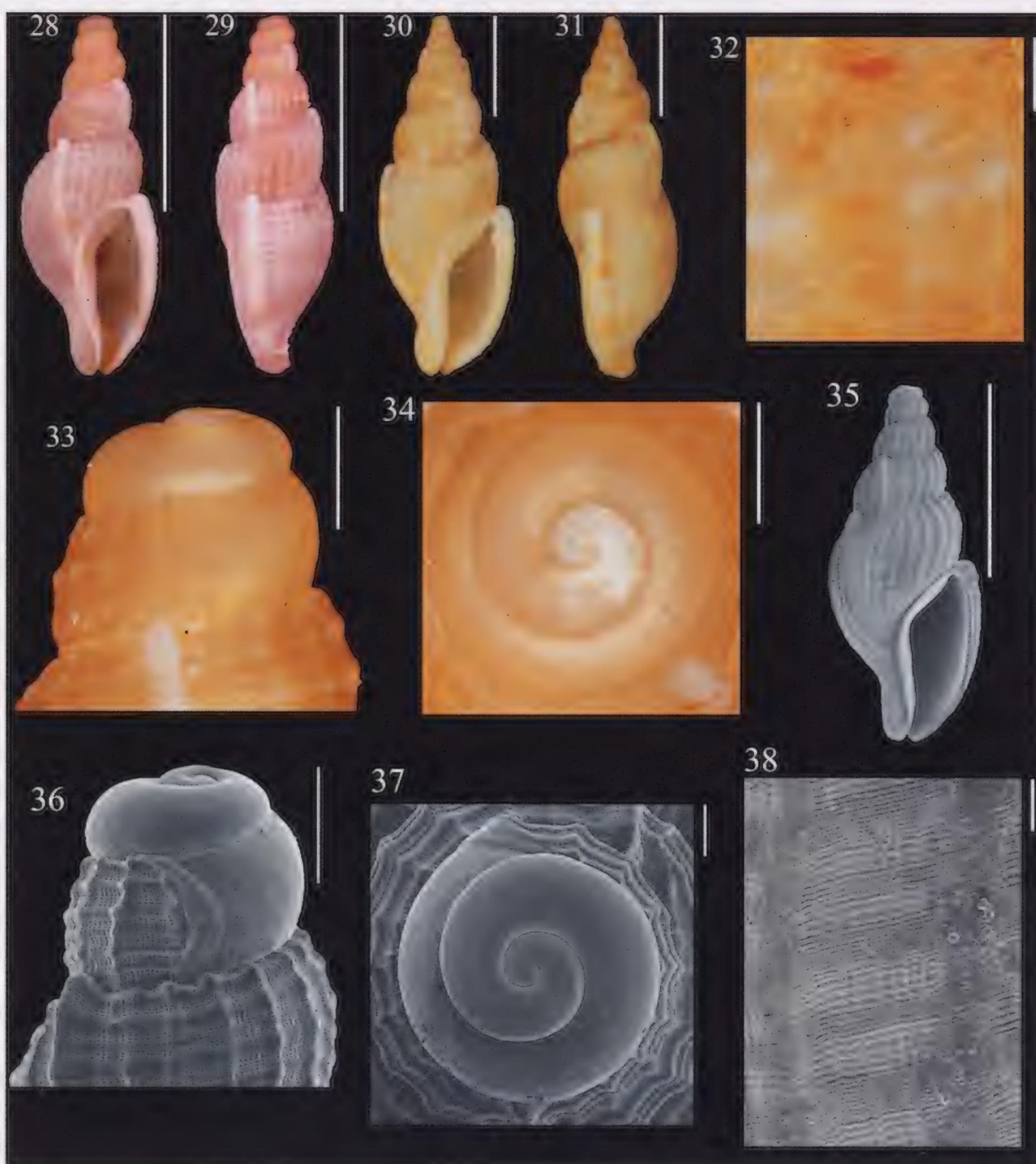
**Other Material examined:** Brazil: Rio Grande do Norte state: BPOT stn. MR45 (04°27'18" S, 37°04'41" W, 47 m), coll. 01/v/2010: MNRJ 34461 [2 sh†]; BPOT stn. MR41 (04°49'39" S, 36°10'08" W, 59 m), coll. 27/x/2009: MNRJ 34462 [1 sh†]; Bahia state: Salvador, Barra (10–15 m), coll. B. Linhares, xii/1992: MNRJ 21547 [6 sh†]; (13°19'52" S, 38°52'52" W, 33 m): MNRJ 27933 [1 sh†]; (13°27'58" S, 38°44'38.40" W): MNRJ 28108 [1 sh†]; (13°27'58" S, 38°46'26.40" W, 35 m): MNRJ 14931 [1 sh†]; (13°28'01.20" S, 38°48'00" W, 30 m): MNRJ 14926 [1 sh†]; (13°28'30" S, 38°48'43.20" W, 30 m): MNRJ 14927 [1 sh†]; (13°29'42" S, 38°48'18" W, 33 m): MNRJ 14928

[1 sh†], MNRJ 34464 [1 sh†]; (13°30'43" S, 38°49'08.40" W, 29 m): MNRJ 28848 [1 sh†]; REVIZEE Central V stn. 5R (15°34'05"S, 38°49'48" W, 20 m), coll. 25/x/1997: IBUFRJ 12282 [1 sh†]; REVIZEE Central I stn. C76 (15°53'49" S, 38°31'05" W, 66 m), coll. 30/iv/1996: IBUFRJ 9186 [1 sh]; IBUFRJ 10115 [1 sh]; Off Nova Viçosa, Abrolhos reef (17°57'58"S 38°42'18"W), coll. P. Young and C. B. Castro, 19/iii/1993: MNRJ 10167 [1 spm†]; REVIZEE Central V stn. 16R (18°03'32"S 37°18'54"W, 100 m), coll. 29/vi/2001: IBUFRJ 14437 [1 sh]; REVIZEE Central I stn. C66 (18°19'59" S, 38°55'01" W, 41 m), coll. 26/iv/1996: IBUFRJ 9069 [1 sh]; Espírito Santo state: REVIZEE Central I stn. VV38 (19°28'26"S, 38°22'30" W, 71 m), coll. 29/ii/1996: IBUFRJ 9809 [1 sh]; REVIZEE Central I stn. D39 (19°28'41" S 38°22'26"W, 84 m), coll. 29/ii/1996: IBUFRJ 7755 [1 sh]; REVIZEE Central I stn. VV24 (20°00'18" S, 39°54'36" W, 45 m), coll. 27/ii/1996: IBUFRJ 13027 [1 sh]; REVIZEE Central VI stn. Y7 (20°50'56" S, 40°10'01" W, 75 m), coll. 28/vi/2002: IBUFRJ 16324 [1 sh]; REVIZEE Central II stn. 35R (20°52'01" S, 40°10'01" W, 55 m), coll. 03/xi/1997: IBUFRJ 12367 [1 sh]; AMBES 7 stn. A2 (21°03'29" S, 40°22'59" W, 40 m): MNRJ 34945 [1 spm†]; Rio de Janeiro state: Arraial do Cabo, Forno beach: (22°57'58" S, 42°00'54" W), coll. M.R. Sá and G. Nunan, 18/xii/1983: MNRJ 14521 [1 sh†]; Arraial do Cabo, Prainha beach, coll. P.M.S. Costa: MNRJ 22245 [1 sh†]; (22°57'58" S, 42°00'39" W, 6 m), coll. 18/iii/2005: MZSP 49326 [1 sh]; São Paulo state: Ilhabela, Vitória Island (~23°44'59" S, 45°01'00" W, 3–10 m), coll. 06/xii/2012: MZSP 109352 [3 spm].

**Measurements:** Holotype, MORG 28659: Whorls= 5.5; SL= 9.2 mm; BWL= 6.2 mm; AL= 4.4 mm; SW= 3.6 mm; AW= 2.1 mm; PCH= not measured; PCW= not measured; SL/SW= 2.6; Paratype USNM 860521: Whorls= 7.0; SL= 18.0 mm; BWL= 12.0 mm; AL= 7.8 mm; SW= 6.9 mm; AW= 4.0 mm; PCH= 0.9 mm; PCW= 1.0; SL/SW= 2.6.

**Distribution:** Brazil: Rio Grande do Norte (present study); Bahia (Harasewych et al., 1992; this study); Vitoria-Trindade Seamount Chain (Harasewych et al., 1992); Rio de Janeiro (present study); São Paulo (present study). From 3 m to 100 m.

**Remarks:** Harasewych et al. (1992) pointed out some differences between *T. leali* and *T. lanceolata*, mentioning a “more inflated and thinner shell” in the former. The holotype of *T. leali* (Figures 28, 29) is a relatively young individual, with a stocky appearance, however the species reaches a larger size (MNRJ 21548: one shell reaching 21.2 mm long) and in this case the general shape becomes more elongated and more similar to the shape of *T. lanceolata*. Small specimens of *T. lanceolata* also have a more inflated appearance as noted by Beu and Maxwell (1987: 40). Another difference pointed by Harasewych et al. (1992) was the presence of axial cords more pronounced than the spiral cords in contrast to *T. lanceolata*. All the shells of *Tritonoharpa* from Brazil examined in the



**Figures 28–34.** *Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992. **28, 29.** Holotype, MORG 28659; **30–34.** Paratype, USNM 860521. **35, 38.** MNRJ 34462. **36, 37.** MNRJ 34461. **28, 30, 35.** Entire shell in frontal view. **29, 31.** Entire shell in lateral view. **32, 38.** Detail of teleoconch sculpture. **33, 36.** Detail of protoconch in lateral view. **34, 37.** Detail of protoconch in apical view. Scale bars: **28–31, 35** = 5 mm; **32, 33** = 500  $\mu$ m; **38** = 100  $\mu$ m.

present study, except for the newly described species, are more similar to the pattern of sculpture described by Harasewych et al. (1992) for *T. leali*, despite being slightly thinner (Figure 38) than in the holotype (Harasewych et al., 1992: fig. 6). Thus, the occurrence of *T. lanceolata* in Brazil is considered dubious and previous records are probably misidentifications of *T. leali*.

*Tritonoharpa leali* was known from the central coast of Brazil from Bahia to Espírito Santo states, and also at the Vitória-Trindade seamount chain (Leal, 1991; Harasewych et al., 1992; Absalão et al., 2006; Rios, 2009). In the present study, the geographic distribution of *T. leali* is extended northwards to the state of Rio Grande do Norte ( $\sim$ 04°S) and southwards to the state of São Paulo ( $\sim$ 23°S), both in Brazil.

One live specimen photographed at Arraial do Cabo, Rio de Janeiro, Brazil, and here identified as *T. leali* is

densely spotted of orange in the head-foot area and the tentacles are almost completely orange (Figure 39). This color pattern was also described by Modica et al. (2009) for a shell identified as “*T. antiquata* (Hinds, 1844)” but it actually belongs to a species complex of *T. angasi* (Braziel, 1877) (Modica et al., 2011a: 121, 2011b: 692). The head-foot of specimens identified as *T. lanceolata* from Guadeloupe, illustrated by Lamy and Pointier (2017: 528, text-fig), and from areas near Peanut Island, Florida, figured at the website of Bill Frank ([www.jaxshells.org/tlance5.htm](http://www.jaxshells.org/tlance5.htm)), also have a very similar color pattern. This color pattern seems common in the genus. It is also possible to observe a large and flattened penis in the Brazilian specimen (Figure 39), similar to the penis of “*T. antiquata*” (Modica et al., 2009: fig. 7P). A more detailed comparison of the penial morphology is limited by the condition of each specimen (alive vs. preserved).



**Figure 39.** *Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992: live specimen photographed at Prainha, Arraial do Cabo, RJ, Brazil (Photo by P.M.S. Costa), observed under a rock. Black arrow indicates the penis.

### ***Tritonoharpa janowskyi* Petuch and Sargent, 2011 (Figures 40–44)**

*Tritonoharpa janowskyi* Petuch and Sargent, 2011: 177, pl. 5, fig. D.

*Tritonoharpa janowskyi* Petuch and Sargent, 2011 – Petuch (2013: 42, fig. 3.7F [reproduced from original illustration])

**Type Locality:** USA: Florida: Palm Beach County, Off Palm Beach Island, 120 m.

**Type Material: Holotype:** USNM 1152535 (sh; here examined).

**Measurements:** Holotype, USNM 1152335: Whorls = 7.5; SL = 16.0 mm; BWL = 11.0 mm; AL = 8.0; SW = 7.3 mm; AW = 4.0 mm; PCH = 1.1 mm; PCW = 1.1 mm; SL/SW = 2.2.

**Distribution:** Only known from the type locality.

**Remarks:** Petuch and Sargent (2011) referred exclusively to the holotype (Figures 40–44) and just a “few other specimens” from the type locality. No other additional record of the species was reported.

*Tritonoharpa janowskyi* is similar in shape to *T. bayeri* (Figures 23–27), as both have a stocky appearance. The former can be distinguished from *T. bayeri* by the proportionally smaller length and width of the teleoconch, by the thicker varices and by the higher number of axial cords between varices (30 vs. 16–18) (Petuch, 1987; Petuch and Sargent, 2011). *Tritonoharpa janowskyi* has a violet color in the protoconch (Figures 42, 43) while *T. bayeri* has a colorless protoconch (Figures 25, 26), but this difference may be due to the conservation status of the shells. The teleoconch of both species has a similar color pattern of irregular brownish patches (Figures 23, 24, 27, 40, 41, 44).

*Tritonoharpa janowskyi* differs from *T. leali* in having proportionally bigger dimensions comparing the holotypes of both species. Furthermore, the spiral cords are

more pronounced than axial cords in *T. janowskyi* in contrast to *T. leali*, and the former reaches a higher number of axial cords between varices (30 vs. 22).

### DISCUSSION

The present overview of *Tritonoharpa* from the western Atlantic demonstrates that there are doubts in the delimitation of most species and a more complete taxonomic revision is necessary. The newly described species, *T. curvapex*, is the most easily recognizable species presenting a distinctive protoconch shape (Figures 4, 9). The other species were rarely reported in the literature, except *T. lanceolata*, and were described based on a few or unique specimens. As commented by Verhecken (2011), who studied species of *Tritonoharpa* from the Philippines, the identification at species level in *Tritonoharpa* is rather complicated. Modica et al. (2011b: 692) also pointed about the difficulties in the taxonomy of *Tritonoharpa* species from shallow and deeper waters of the Pacific, Indian and Atlantic Oceans.

Although we recognized some diagnostic shell features of most of the *Tritonoharpa* from the western Atlantic, the scarcity of individuals hinders description of the variability of these features. *Tritonoharpa lanceolata* is supposedly the most common species, despite uncertainties about its taxonomy, and shows a variable teleoconch sculpture and color pattern (Beu and Maxwell, 1987). More recently, Lamy and Pointier (2017: 528, pl. 184, figs. 8–14) identified two nominal species (*T. bayeri* and *T. lanceolata*) and five morphotypes of *Tritonoharpa* sp. from Guadeloupe (Caribbean). These authors did not describe the diagnostic features of each morphotype, but based on the illustrations they possibly considered the different color patterns in the shells. At present, distinction of species by color pattern is a dubious approach.

Knowledge about the anatomy of *Tritonoharpa* is even more scarce, in the present study a few specimens of *T. leali* with soft parts were originally available for study. Unfortunately, part of these specimens was destroyed in the fire of “Museu Nacional” prior to anatomical studies. A *Tritonoharpa* species from the Philippines, erroneously cited as *T. antiquata* (Modica et al., 2009, 2011a, 2011b), is the only species of the genus of which the anatomy is known. More investigations on the anatomy of *Tritonoharpa* may help in the species delimitation.

Thus, based on the material examined here we can conclude that two species of *Tritonoharpa* certainly occur in Brazil: *T. curvapex* and *T. leali*. *Tritonoharpa leali* has a wider range of distribution in the Brazilian coast than previously reported in the literature, with occurrences in most of the Tropical Southwestern Atlantic province. However, it is possible that we were unable to recognize more than one species under the name *T. leali* in the present overview. The occurrence of *T. lanceolata* in Brazil needs clarifications.

The protoconch of all species of *Tritonoharpa* from the western Atlantic indicates a lecithotrophic development by



**Figures 40-44.** *Tritonoharpa janowski* Petuch and Sargent, 2011: holotype, USNM 1152535. **40.** Entire shell in frontal view. **41.** Entire shell in lateral view. **42, 43.** Detail of protoconch in lateral and apical views, respectively. **44.** Detail of teleoconch sculpture. Scale bars: **40, 41** = 5 mm; **42, 43** = 500  $\mu$ m; **44** = 400  $\mu$ m.

its diameter and number of whorls, which may explain the restricted geographic distribution of most species. *Tritonoharpa lanceolata* differs from the remaining species by its wider distribution, but as discussed above, this distribution is possibly over estimated based on the doubts about the identity of this species.

We hope that the illustrations of specimens, including type material whenever possible, and the gathering of data about western Atlantic *Tritonoharpa* will be useful for future studies about this genus, despite some of the tentative identifications in a confusing taxonomic scenario.

#### ACKNOWLEDGMENTS

We are grateful to Gary Rosenberg, Paul Callomon, and Nasreen Phillips (ANSP), Amanda Bemis and John Slapcinsky (FLMNH), Cleo Oliveira (IBUFRJ), José Espinosa (Instituto de Oceanología, Cuba), Alexandre Pimenta (MNRJ), Paula Spotorno-Oliveira and the late Eliézer de C. Rios (MORG), Luiz Simone (MZSP), Sigrid Hof (SMF), Ellen Strong and Yolanda Villacampa (USNM) for access to collections, loan of specimens, photographs and/or information regarding type material. We thank André Verhecken (RBINS), José H. Leal (BMSM), Jean-François Lesport and Jean-Michel Pacaud (MNHN), Rodrigo Salvador (MNZ, Te Papa Tongarewa) for providing important literature concerning Cancellariidae. Many thanks to M.G. Harasewych (USNM) and André Verhecken for providing critiques that improved the manuscript. We appreciate the support of C. Messias (MN-UFRJ) for SEM operation. Thanks to Petrobrás SA for the material collected during BPOT MR and AMBES projects. The senior author very much appreciates the support of his friends Carine Gonçalves and Gustavo Miranda during a research visit to the USA.

#### LITERATURE CITED

Absalão, R.S., C.H.S. Caetano, and R.R. Fortes. 2006. Filo Mollusca. In: Lavrado, H.P. and B.L. Ignacio (eds.) Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira. Museu Nacional, Rio de Janeiro, pp. 211-260.

Altena, C.O.R. 1975. The marine Mollusca of Suriname (Dutch Guiana) Holocene and Recent. Part III. Gastropoda and Cephalopoda. Zoologische Verhandelingen 139: 104 pp., 11 pls.

Barros, J.C.N. and R.E. Petit. 2007. A new species of *Microcancilla* (Gastropoda: Cancellariidae) from the continental slope off northeastern Brazil. The Nautilus 121 (2): 95-98.

Barros, J.C.N. and S.F.B. Lima. 2007. Three new species of Cancellariidae (Gastropoda: Neogastropoda) from northeast Brazil with first record of *Gergovia* for the Atlantic ocean. Zootaxa 1387: 59-68.

Beu, A.G. and P.A. Maxwell. 1987. A revision of the fossil and living gastropods related to *Plesiotriton* Fischer, 1884 (Family Cancellariidae, Subfamily Plesiotritoninae n. subfam.) with an Appendix: Genera of Buccinidae, Pisaniinae related to *Colubraria* Schumacher, 1817. New Zealand Geological Survey Paleontological Bulletin 54: 1-140, pls. 1-30.

Bouchet, P., J-P. Rocroi, B. Hausdorf, A. Kaim, Y. Kano, A. Nützel, P. Parkhaev, M. Schrödl, and E.E. Strong. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61 (1-2): 1-526.

Daccarett, E.Y. and V.S. Bossio. 2011. Colombian seashells from the Caribbean Sea. L'Informatore Piceno, Italia. 384 pp, 150 pls.

Espinosa, J., J. Ortea, R. Sánchez, and J. Gutiérrez. 2012. Moluscos marinos. Reserva de la Biosfera de la

Península de Guanahacabibes. Instituto de Oceanología, Habana, Cuba. 325 pp.

Harasewych, M.G. and R.E. Petit. 2011. Two new species of Admetinae (Gastropoda: Cancellariidae) from the northeastern Pacific Ocean. *The Nautilus* 125 (3): 159–163.

Harasewych, M.G., R.E. Petit, and A. Verhecken. 1992. Two new species of Cancellariidae (Gastropoda: Neogastropoda) from Brazil. *The Nautilus* 106 (2): 43–49.

Iredale, T. 1929. Queensland molluscan notes, no. 1. *Memoirs of the Queensland Museum* 9 (3): 261–297, pls. 30–31.

Kohn, A.J. 1988. Type specimens and identity of the described species of *Conus*. VIII. The species described 1821–1830. *Zoological Journal of the Linnean Society* 93 (1): 19–70.

Lamy, D. and J-P. Pointier. 2017. Marine and freshwater molluscs of the French Caribbean, Volumes 1–2. PLB Editions, Beta, Guadeloupe. 785 pp.

Leal, J.H. 1991. Marine Prosobranch Gastropods from Oceanic Islands off Brazil: Species composition and Biogeography. Universal Book Services, Oegstgeest, x + 418 pp.

Lee, H.G. 2009. Marine Shells of Northeast Florida. Jacksonville Shell Club, Inc, Jacksonville, 204 pp.

Lima, S.F.B., J.C.N. Barros, and E.R. Petit. 2007. A new species of *Gerdieilla* (Gastropoda: Cancellariidae) from the South Atlantic Ocean off Brazil with discussion of an undescribed species. *The Nautilus* 121 (2): 99–103.

Lyons, W.G. 1989. Nearshore Marine Ecology at Hutchinson Island, Florida: 1971–1974. XI. Mollusks. Florida Marine Research Publications, St. Petersburg (Florida), 131 pp.

Lyons, W.G. 1998. Checklist of Shallow-Water Marine Mollusca of Florida. In: D. K. Camp, W.G. Lyons, and T.H. Perkins (eds.). Checklists of selected shallow-water marine invertebrates of Florida. St. Petersburg, Florida. Florida Marine Research Institute, Technical Report TR-3, pp. 5–78.

Modica, M.V., A.R. Kosyan and M. Oliverio. 2009. The relationships of the enigmatic gastropod *Tritonoharpa* (Neogastropoda): New data on early neogastropod evolution? *The Nautilus* 123 (3): 177–188.

Modica, M.V., A. Verhecken and M. Oliverio. 2011a. The relationships of the enigmatic neogastropod *Loxotaphrus* (Cancellariidae). *New Zealand Journal of Geology and Geophysics* 54: 115–124.

Modica, M.V., P. Bouchet, C. Cruaud, J. Utge, and M. Oliverio. 2011b. Molecular phylogeny of the nutmeg shells (Neogastropoda, Cancellariidae). *Molecular Phylogenetics and Evolution* 59: 685–697.

MolluscaBase. 2018. *Tritonoharpa* Dall, 1908. Available at: <http://www.molluscabase.org/aphia.php?p=taxdetails&id=416105>, on 31 October 2018.

MolluscaBase. 2020. Cancellariidae Forbes and Hanley, 1851. Available at: <http://www.molluscabase.org/aphia.php?p=taxdetails&id=13600>, on 18 November 2020.

Mörch, O.A.L. 1877. *Synopsis molluscorum marinorum Indiarum occidentalium imprimis insularum danicarum (contin.). Malakozoologische Blätter* 24: 14–66, 93–123.

Pacaud, J.M., D. Ledon, and P. Loubry. 2015. Les Plesiotritoninae (Mollusca, Gastropoda, Cancellariidae) de l’Eocène du bassin de Paris, du Cotentin, de Loire-Atlantique et d’Aquitaine. *Palaeontos* 27: 65–119.

Perry, L.M. and J.S. Schwengel. 1955. *Marine Shells of the Western Coast of Florida*. Paleontological Research Institute, Ithaca, New York. 318 pp.

Petit, R.E. and M.G. Harasewych. 1990. Catalogue of the superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia). *The Nautilus* (Supplement 1): 1–69.

Petit, R.E. and M.G. Harasewych. 2005. Catalogue of the superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia) – 2<sup>nd</sup> edition. *Zootaxa* 1102: 1–161.

Petuch, E.J. 1987. *New Caribbean Molluscan Faunas*. The Coastal Education and Research Foundation, Charlottesville, 154 pp., 29 pls; addendum 2 pp., 1 pl.

Petuch, E.J. 2013. *Biogeography and Biodiversity of Western Atlantic mollusks*. CRC Press, Boca Raton, 252 pp.

Petuch, E.J. and D.M. Sargent. 2011. *Rare and Unusual Shells of the Florida Keys and Adjacent Areas*. MdM Publishing, Florida. 189 p.

Redfern, C. 2013. *Bahamian Seashells*. 1161 species from Abaco, Bahamas. Bahamianseashells.com, Inc., Boca Raton, 501 pp.

Rios, E.C. 1970. *Coastal Brazilian Seashells*. Museu Oceanográfico do Rio Grande, Rio Grande, Rio Grande do Sul, Brazil. 255 p., 50 pls.

Rios, E.C. 1975. *Brazilian Marine Mollusks Iconography*. Museu Oceanográfico do Rio Grande, Rio Grande, Rio Grande do Sul, Brazil. 331 pp., 91 pls.

Rios, E.C. 1985. *Seashells of Brazil*. Editora da Fundação Universidade Rio Grande, Rio Grande, Rio Grande do Sul, Brazil. 328 pp., 102 pls.

Rios, E.C. 1994. *Seashells of Brazil*, 2<sup>nd</sup> Edition. Editora da Fundação Universidade Rio Grande, Rio Grande, Rio Grande do Sul, Brazil. 368 pp., 113 pls.

Rios, E.C. 2009. *Compendium of Brazilian Seashells*. Evangraf, Rio Grande, Rio Grande do Sul, Brazil. 668 p.

Rosenberg, G., F. Moretzsohn, and E.F. García. 2009. *Gastropoda (Mollusca) of the Gulf of Mexico*. pp. 579–699. In: Felder, D.L. and D.K. Camp (eds.) *Gulf of Mexico: origins, waters, and biota*. Vol. 1. Biodiversity. Texas A&M University Press, College Station, 1393 p.

Simone, L.R.L. and A. Birman. 2006. A new species of *Iphinopsis* (Caenogastropoda, Cancellariidae) from Brazil. *Journal of Conchology* 39 (2): 141–144.

Tunnel Jr., J.R., J.W. Andrews, N.C. Barrera, and F. Moretzsohn. 2010. *Encyclopedia of Texas Seashells – Identification, Ecology, Distribution and History*. Harte Research Institute for Gulf of Mexico Studies, Series xi, Corpus Christi, 512 pp.

Verduin, A. 1982. How complete are diagnoses of coiled shells of regular build? A mathematical approach. *Basteria* 45 (6): 127-142.

Verhecken, A. 1991. Description of two new species of bathyal Cancellariidae (Mollusca, Gastropoda) from off Brazil. *Bulletin du Muséum national d'histoire naturelle (série 4)* 12 (3-4): 547-553.

Verhecken, A. 2007. Revision of the Cancellariidae (Mollusca, Neogastropoda, Cancellarioidea) of the eastern Atlantic (40°N-40°S) and the Mediterranean. *Zoosystema* 29 (2): 281-364.

Verhecken, A. 2011. The Cancellariidae of the PANGLAO Marine Biodiversity Project 2004 and the PANGLAO 2005 and AURORA 2007 deep sea cruises in the Philippines, with the description of six new species (Neogastropoda, Cancellarioidea). *Vita Malacologica* 9: 1-60.

Vokes, H.E. and E.H. Vokes. 1983. Distribution of Shallow-Water Marine Mollusca, Yucatan Peninsula, Mexico. *Mesoamerican Ecology Institute Monograph 1. Middle American Research Institute Publication 54.* Tulane University, New Orleans. viii + 183 pp.

Wolfe, D.A. 2008. Mollusks taken by Beam Trawl in the vicinity of Gray's Reef National Marine Sanctuary on the Continental Shelf off Georgia, Southeastern U.S. NOAA Technical Memorandum NOS NCCOS 88. 40 pp.

[www.jaxshells.org/tlance5.htm](http://www.jaxshells.org/tlance5.htm). Accessed on 03 April 2020.

Zamudio, K.R., A. Kellner, C. Serejo, M.R. Britto, C.B. Castro, P.A. Buckup, D.O. Pires, M. Couri, A.B. Kury, I.A. Cardoso, M.L. Monné, J. Pombal Jr., C.M. Patiú, V. Padula, A.D. Pimenta, C.R.R. Ventura, E. Hajdu, J. Zanol, E.M. Bruna, J. Fitzpatrick and L.A. Rocha. 2018. Lack of Science support fails Brazil. *Science* 361 (6409): 1322-1323.

Zilch, A. 1967. Geschichte der malakologischen Sektion. *Archiv für Molluskenkunde* 97 (1): 7-43.

# Memorial to Warren O. Addicott—A remarkable student of Tertiary marine mollusks of the northeastern Pacific

**Charles L. Powell, II**

U.S. Geological Survey, Menlo Park, CA 94025  
powell2@sbcglobal.net

**Kevin J. Meade**

California State University, Fullerton  
Fullerton, CA 92831 USA  
kevjmeade01@csu.fullerton.edu

## ABSTRACT

Warren Oliver Addicott (1930–2009) was a prolific molluscan paleontologist who produced in excess of one hundred publications, most of which deal with Tertiary fossil mollusks from western North America. In these publications he is credited with naming more than 80 new molluscan taxa, and recognizing and illustrating an additional 17 taxa that lacked sufficient material to be described as new. In addition, he is honored in having nine species named for him (eight mollusks and one arthropod).

"Warren Addicott was an exemplary paleontologist, far ahead of his peers, and willing to move into new areas and issues. He helped to supervise the Circum-Pacific Map Project, with many maps being put together and published under his tenure." (Ellen J. Moore, 2010, pers. comm., October 2010)

"...Warren Oliver Addicott (Ph.D. 1956), whose career with the Paleontology and Stratigraphy Branch of the U.S. Geological Survey in Menlo Park set new standards for monographic systematics, faunal and biostratigraphic documentation, and photographic illustration as well as initiating new insights and integration of molluscan research with active margin tectonics, refined climate curves, latitudinal distributions based on marine mollusks, increased radiometric age control on molluscan faunas, extension of molluscan paleontological interpretations into Alaska, and fostering exchange and collaboration with Japanese molluscan paleontologists." (Hickman, 2009.)

## MEMORIAL

Warren Addicott was born in Fresno, California on February 17, 1930 to Irwin and Astrid Addicott. He was the eldest of two brothers, the younger being Alan Addicott. His formative years were spent in California where he attended Fresno High School in Fresno. At Fresno High School he played basketball making the local "Fresno Bee's [newspaper] All Yosemite League Basketball Team" (The Fresno Bee newspaper, February 27, 1946: 11; <https://www.newspapers.com/clip/8987288/the-fresno-bee-the-republican/>). Afterward he attended Pomona College, where he was a student of the founding director of the geology department, Alfred O. Woodford. Warren graduated in 1951 with a BA in geology. A year later he received his M.A. from Stanford University's Hopkins Marine Station in Pacific Grove, California. Subsequently he attended the University of California at Berkeley where he received his Ph.D. from the Museum of Paleontology in 1956. While there, Warren completed his pioneering work on the Neogene Kern River deposits (1956) under J. Wyatt Durham, Charles W. Gilbert, and Ralph L. Langenheim.

In 1962, Warren joined the then-expanding Paleontology and Stratigraphy Branch of the U.S. Geological Survey (USGS) in Menlo Park, California. There he had a long and illustrious career focused on molluscan fossils of the eastern Pacific collaborating with colleagues in the Russian Far East, Japan, and later Spain. His first paper published by the USGS was with Jack G. Vedder, a renowned geologist in his own right, where they discussed the relationship between paleotemperature and Miocene mollusks in the Kern River area. Probably his most prominent publication is "Miocene Gastropods and Biostratigraphy of the Kern River Area, California" (Addicott, 1970d), which, 50 years later, remains a classic and an outstanding publication. In addition to his publications (listed below) Warren authored hundreds of Internal Reports on Referred Fossils (known as E&R's within the USGS) for other federal scientists and scholars around the world. John Barron (USGS) related a memory of Warren to us: when he first started his career at the USGS, he asked Warren for advice on how he should work. Warren suggested he divide his time into thirds, one third on service work (E&R's), one third on collaboration, and one third on his own research. This division of labor has similarly worked well for many USGS paleontologists over the years.

Warren was always willing to aid students and fellow scientists in their work. He sponsored the USGS postdoc of Judith Terry Smith (Smithsonian) for a year, although the two did not interact much. He helped Clifford M. Nelson with his dissertation on the gastropod genus



**Figure 1.** Warren O. Addicott. Photograph courtesy of Eric Addicott.

*Neptunea*. Nelson would later write a letter to Warren thanking him for his help; this letter is now preserved in the archives at the Museum of Paleontology, University of California, Berkeley. Richard G. Stanley (USGS) recalls

that when speaking with Warren in 1973 about his undergraduate thesis, he offered to loan him some fossils that Warren and Joe Clark (Indiana University of Pennsylvania) had collected from Richard's field site. Warren

was also interested in Richard's 1987 poster on right-lateral displacement of the San Andreas fault, which many other scientists disapproved of at the time. "I remember Warren as an exemplary and thoughtful scientist, and as a generous and kind human being," he related to us. Warren always answered letters that Lindsey Groves (Natural History Museum of Los Angeles County) sent him, as this latter worked on his masters thesis at California State University, Northridge. In addition, whenever possible he joined Robert J. McLaughlin and Dave Durham (both USGS) on field trips to Salinas Valley localities, and was always willing to look at "the most scruffy material." James C. Ingle, Jr. (Stanford University) tells of how he worked with Warren on several US-Japan projects dealing with Neogene paleontology around the Pacific Rim and that he later helped Jim obtain funding for field work on the Burica Formation in Panama. "He was a premier paleontologist, a wonderful colleague, and simply a great human being in every respect," he recalled.

In 1971, Warren became a consulting Associate Professor of Geology at Stanford University where he served as counsel for graduate students and supervised the University's Cenozoic and modern mollusk collections. Around 1980, Warren left the Branch for Paleontology and Stratigraphy, joining the Circum-Pacific Map Project (C-P M Project), because he was tired of having to ask for money from projects he helped. The goal of the C-P M Project was to gather together scientists from different parts of the world toward developing geologically significant maps throughout the Pacific region. Warren was appointed General Chairman of the C-P M Project in 1983, taking over from John A. Reinemund, who had been appointed Director in 1982. A few years later, in 1986, Warren retired from the USGS. That same year, he and his second wife Suzanne Aubin moved to Ashland, Oregon. After moving, Warren taught at the University of Southern Oregon from 1986 until his final retirement in 1990.

Throughout his career Warren was heavily involved in the broader scientific community. He became a fellow of the California Academy of Sciences, gave lectures and lead field trips for the American Association of Petroleum Geologists (AAPG) along with being editor of the Pacific Petroleum Geologists, a newsletter of the Pacific Section AAPG, and from 1971 to 1981 was a Trustee of Bulletins of American Paleontology (Paleontology Research Institute, Ithaca, New York). He was a founding member of the Western Society of Malacologists (1968) and is believed to have regularly attended meetings until at least 1975. In 1970, Warren was elected Secretary of the Paleontological Society, a position he held until 1976. Later, he was elected President of the Paleontological Society (1980). He also served on the editorial board for *The Veliger*, a quarterly published by the California Malacozoological Society, Inc.

When not working on research, Warren loved to garden. He was vice-president of the Peninsula Camelia Society in 1964 after moving to Menlo Park for his job at the USGS. In 1964 and again in 1968 he won several

camellia growing contests run by the local camellia society (Southern California Camellia Society, 1964: 22; 1968: 9–18), and wrote about the subject in the specialized literature (Addicott, 1967d: 27.)

He was also skilled at ceramics and a talented poet. Warren loved music, especially blues and jazz, and loved to compose his own music that he would play on the piano. He was married twice, first to Susanne Smith (1955–1972), and later to Suzanne Aubin (1976–2009). He left two children, Eric Addicott and Carol Kral, as well as two stepchildren, David LeDrew and Christine LeDrew-Johnson. Eric recounted to us: "Dad made it a priority to spend lots of time with my sister and me, and in many ways the divorce enhanced his relationship with us. He was always so loving and caring, and he always trusted my judgment and never really tried to guide or advise me too much. He introduced me to fishing, backpacking, cycling, and skiing, activities which I still do."

Warren was a world traveler and took an avid interest in other cultures. Not only did he travel for research-related reasons, but also for pleasure. He would even take time during overseas scientific conferences to visit scenic locations. For example during the 1971 Mediterranean Neogene Congress in Lyon, France, he visited the Rhone and Bordeaux basins in France.

After his retirement he moved to Ashland, where he continued to travel. In 1997, he wrote a letter to the Nu Alpha Phi fraternity at Pomona College (of which he was a member during his time there) noting that he and his second wife Suzanne had traveled to India in 1996 and stayed there for three months. He also worked as a realtor while in Ashland to keep busy.

Warren O. Addicott passed away July 11, 2009, with his wife Suzanne by his side, from complications of cancer. A hard worker and kind man, he named over 80 new molluscan taxa during his lifetime. His contributions to molluscan paleontology, and paleontology in general, solidified Warren Addicott's name as one of the great paleontologists of the late 20th Century.

#### NEW SPECIES NAMED IN HONOR OF WARREN O. ADDICOTT (names presented as in original combinations)

##### **Mollusca**

##### **Bivalvia**

*Macoma addicotti* Nikas (1977)

*Mactromeris addicotti* Kanno (1971)

*Modiolus addicotti* Moore (1984)

*Mytilus (Tumidomytilus) addicotti* Kafanov (1985) –

Holotype figured by Allison and Addicott (1976), pl. 3, fig. 9 [= *My. addicotti*]

*Pitar addicotti* Zinsmeister (1983)

##### **Cephalopoda**

*Moroteuthis addicotti* Clarke and Fitch (1979)

##### **Gastropoda**

*Nassarius grammatus addicotti* Adegoke (1969)

##### **Scaphopoda**

*Cadulus (Platyschides?) addicotti* Emerson (1957)

**Arthropoda**

**Crustacea**

*Balanus addicotti* Zullo (1979)

NEW MOLLUSCAN NAMES PROPOSED BY  
WARREN O. ADDICOTT

**Bivalvia**

*Nucula salmonensis* Addicott, 1966c

*Platyodon colobus fowleri* Addicott, 1966c

*Propeamussium (Propeamussium) leohertleini* Addicott, 1971a

**Gastropoda**

*Acteon (Rictaxis) weaveri* Addicott, 1970d

*Aforia clallamensis tricarinata* Addicott, 1966c

*Antillophos woodringi* Addicott, 1970d

*Austrotrophon kernensis medialis* (Addicott, 1970d)

*Balcis lutzi* Addicott, 1970d

*Balcis petrolia* Addicott, 1970d

*Barkeria* Addicott, 1970d – as a subgenus of *Cancellaria*

*Calicantharus rancherianus* Addicott, 1970d

*Calicantharus woodfordi* Addicott, 1970d

*Callostoma carsoni* Addicott, 1970d

*Calyptitraea coreyi* Addicott, 1970d

*Cancellaria (Crawfordina) kernensis* Addicott, 1970d

*Cancellaria (Euclia) circumspinosa* Addicott, 1970d

*Cancellaria (Euclia) ocoyana* Addicott, 1970d

*Cancellaria (Narona) birchi* Addicott, 1970d

*Cancellaria galei* Addicott, 1970d

*Cancellaria keenae* Addicott, 1970d

*Catilon* Addicott, 1965c – a subgenus of *Nassarius*

*Crassispira olcesensis* Addicott, 1970d

*Crepidula bractea* Addicott, 1970d

*Crucibulum (Dispotaea) papulum* Addicott, 1970d

*Demondia* Addicott, 1965c – a subgenus of *Nassarius*

*Epitoonium (Gyroscala) barkerianum* Addicott, 1970d

*Epitonium (Nitidscala) tedfordi* Addicott, 1970d

*Forreria emersoni* Addicott, 1970d

*Gibbula (Tumulus?) baileyi* Addicott, 1970d

*Glyphostoma carinata* Addicott, 1970d

*Haminoea articensis* Addicott, 1966c

*Kelletia lorata* Addicott, 1970d

*Knefastia grarcesana* Addicott, 1970d

*Mangelia (Notocytharella?) hartensis* Addicott, 1970d

*Mitra (Atrimitra) andersoni* Addicott, 1970d

*Mitrella (Columbellopsis) alta* Addicott, 1970d

*Morula (Morunella) granti* Addicott, 1970d

*Nassarius (Catilon) smooti* Addicott, 1965c

*Nassarius hoquiamensis* Addicott, 1966c

*Nassarius (Phrontis) harrellensis* Addicott, 1970d

*Nassarius (Phorntis?) posoensis* Addicott, 1970d

*Nassarius (Catilon?) salinasensis* Addicott, 1965c

*Natica vokesi* Addicott, 1966c

*Nerita (Theliostyla?) joaquinensis* Addicott, 1970d

*Niso cottonwoodensis* Addicott, 1970d

*Ocenebrina clarki* (Addicott, 1970d)

*Odostomia (Chrysallida?) sequoiana* Addicott, 1970d

*Odontomia (Menestho) repenningi* Addicott, 1970d

*Polystira englishi* Addicott, 1970d

*Scaphander dollaris* Addicott, 1966c

*Sulcoretusa? israelski* Addicott, 1970d

*Tectionatica? satsopensis* Addicott, 1966c

*Tegula ellenae* Addicott, 1966c

*Tegula (Omphalius) dalli arnoldi* Addicott, 1970d

*Tegula (Omphalius) laevis* Addicott, 1970d

*Terebra (Fusoterebra?) adelaideana* Addicott, 1970d

*Terebra (Strioterebrum) stirtoni* Addicott, 1970d

*Trochotropis tricarinata* Addicott, 1970d

*Trochotropis (Iphinoe) goweri* Addicott, 1966c

*Turbanilla (Chemnitzia) hannali* Addicott, 1970d

*Turbanilla hormigacuesta* Addicott, 1970d

*Turbanilla (Tragula) greenhomensis* Addicott, 1970d

*Turbanilla (Ptycheulimella) edisonensis* Addicott, 1970d

*Turritella kernensis* Addicott, 1970d

*Turritella (Idaella) vaquinana* Addicott, 1966c

*Volvuella joaquinensis* Addicott, 1970d

In addition to the species named by Warren (above) he recognized and illustrated a number of other potential new species. Unfortunately, these possible new species were not represented by sufficient material for him to name them and are listed in his publications simply as new species (n. sp.), or new species? (n. sp.?).

**Bivalvia**

*Macoma* n. sp. Addicott, 1969a [= *M. addicotti* Nikas, 1977]

**Gastropoda**

*Astraea (Pomaulax) n. sp.* Addicott (1970d)

*Cancellaria* n. sp. Addicott, 1969a [= *C. fergusoni* Carson, 1926]

*Cancellaria* n. sp.? aff. *C. alaskensis* Clark (1932), Addicott, 1980

*Cancellaria (Euclia?) n. sp.* Addicott, 1966c

*Cymatium* n. sp. Addicott, 1970d

*Diodora (Diodora) n. sp.* Addicott, 1970d

*Diodora?* n. sp. Addicott, 1970d

*Neverita (Glossaulax) n. sp.?* Addicott, 1970d

*Odostomia (Chrysallida?) n. sp.* Addicott, 1970d

*Odostomia (Evalea?) n. sp.* Addicott, 1970d

*Oliva (Oliva) n. sp.?* Addicott, 1970d

*Terebra (Strioterebrum) n. sp.?* Addicott, 1970d

*Terebra (Terebra) n. sp.* Addicott, 1970d

*Triumphis?* n. sp. Addicott, 1970d

*Turbanilla (Chemnitzia) n. sp.* Addicott, 1970d

*Turbanilla (Chemnitzia?) n. sp.* Addicott, 1970d

*Turbanilla (Pyrgiscus) n. sp.* Addicott, 1970d

PUBLICATIONS OF WARREN O. ADDICOTT

1953

Emerson, W.K., and W.O. Addicott. 1953. A Pleistocene invertebrate fauna from the southwest corner of San Diego County, California. San Diego Society of Natural History Transactions 11(17): 429-444.

**1956**

Addicott, W.O. 1956. Miocene stratigraphy northeast of Bakersfield, California. Berkeley. University of California, Ph.D. dissertation.

**1958**

Emerson, W.K., and W.O. Addicott. 1958. Pleistocene invertebrates from Punta Baja, Baja California, Mexico. American Museum Novitates 1909: 1–11.

**1959**

Addicott, W.O., and W.K. Emerson. 1959. Late Pleistocene invertebrates from Punta Cabras, Baja California, Mexico. American Museum Novitates 1925: 1–33.

**1963**

- a. Addicott, W.O. 1963. An unusual occurrence of *Tresus nuttallii* (Conrad, 1837) (Mollusca: Pelecypoda). The Veliger 5(4): 143–144.
- b. Addicott, W.O. 1963. Interpretation of the invertebrate fauna from the Upper Pleistocene Battery Formation near Crescent City, California. Proceedings of the California Academy of Sciences, Fourth Series 31(13): 341–347.
- c. Addicott, W.O., and J.G. Vedder. 1963. Paleotemperature inferences from late Miocene mollusks in the San Luis Obispo–Bakersfield area, California. U.S. Geological Survey Professional Paper 475C: C63–C68.

**1964**

- a. Addicott, W.O. 1964. A Late Pleistocene invertebrate fauna from southwestern Oregon. Journal of Paleontology 38(4): 650–661.
- b. Addicott, W.O. 1964. Pleistocene invertebrates from the Dune Terrace, western Santa Monica Mountains, California. Bulletin of the Southern California Academy of Sciences 63(3): 141–150.

**1965**

- a. Addicott, W.O. 1965. On the identification of *Schizopyga californiana* Conrad, a California Pliocene gastropod. Proceedings of the California Academy of Sciences, Fourth Series 33(2): 47–58.
- b. Addicott, W.O. 1965. The enigmatic late Cenozoic gastropod *Schizopyga californiana* [abs.]. American Malacological Union, Annual Report for 1964: 44.
- c. Addicott, W.O. 1965. Some western American Cenozoic gastropods of the genus *Nassarius*. U.S. Geological Survey Professional Paper 503B: B1–B24.
- d. Addicott, W.O. 1965. Miocene macrofossils of the southeastern San Joaquin Valley, Calif. U.S. Geological Survey Professional Paper 525C: C101–C109.
- e. Durham, D.L., and W.O. Addicott. 1965. Pancho Rico Formation, Salinas Valley, California. U.S. Geological Survey Professional Paper 524A: A1–A22.
- f. Durham, D.L., and W.O. Addicott. 1965. Upper Miocene and Pliocene marine stratigraphy in southern Salinas Valley, California. U.S. Geological Survey Bulletin 1194: E1–E7.

**1966**

- a. Addicott, W.O. 1966. Late Pleistocene marine paleoecology and zoogeography in central California. U.S. Geological Survey Professional Paper 523C: C1–C21.
- b. Addicott, W.O. 1966. Miocene macrofossils of the southeastern San Joaquin Valley, California. U.S. Geological Survey Professional Paper 525C: C101–C109.
- c. Addicott, W.O. 1966. New Tertiary marine mollusks from Oregon and Washington. Journal of Paleontology 40(3): 635–646.
- d. Repenning, C.A., D.L. Jones, and W.O. Addicott. 1966. Geology of the Great Valley. Mineral Information Service 22(1): 3–6.

**1967**

- a. Addicott, W.O. 1967. Age of the Skooner Gulch Formation, Mendocino County, California. U.S. Geological Survey Bulletin 1254C: C1–C11.
- b. Addicott, W.O. 1967. Zoogeographic evidence for late Tertiary lateral slip on the San Andreas fault, California. U.S. Geological Survey Professional Paper 593D: D1–D12.
- c. Addicott, W.O. 1967. Paleontologic evidence for large post-early Miocene lateral slips on the San Andreas fault, California [abs.]. Geological Society of America, Program, 63rd annual meeting, Santa Barbara, March 22–25, 1967: 17.

**1968**

- a. Addicott, W.O. 1968. Mid-Tertiary zoogeography and paleogeographic discontinuities across the San Andreas fault, California. Pp. 144–165 [in:] W.R. Dickinson and A. Grantz, Proceedings of conference on geologic problems of San Andreas fault system. Stanford University Publications, Geological Sciences 11: 1–387.
- b. Addicott, W.O. 1968. Neogene molluscan zoogeography and climatic change in the northeastern Pacific Ocean [abs.]. Geological Society of America, 1968 Annual Meetings, Program with abstracts: 2–3.
- c. Bradley, W.C., and W.O. Addicott. 1968. Age of first marine terrace near Santa Cruz, California. Geological Society of America Bulletin 79(9): 1203–1210.

**1969**

- a. Addicott, W.O. 1969. Late Pliocene mollusks from San Francisco Peninsula, California, and their paleogeographic significance. Proceedings of the California Academy of Sciences, Fourth Series 37(3): 57–93.
- b. Addicott, W.O. 1969. Late Pliocene marine mollusks from the northeastern Santa Cruz Mountains, California [abs.]. Abstracts with Program for 1969 (Cordilleran Section), Geological Society of America, 3: 1.
- c. Addicott, W.O. 1969. Tertiary climatic change in the marginal northeastern Pacific Ocean. Science 165(3893): 583–586.

d. Addicott, W.O. and S. Kanno. 1969. Current paleontological investigations on Cenozoic marine mollusks of the west coast of North America. *The Veliger* 12(1): 135-139.

e. Hopkins, D.M., D.W. Scholl, W.O. Addicott, R.L. Pierce, P.B. Smith, J.A. Wolf, D. Gershonovich, B. Kotenev, K.E. Lohman, J.H. Lipps, and J. Obradovich. 1969. Cretaceous, Tertiary, and early Pleistocene rocks from the continental margin in the Bering Sea. *Geological Society of America Bulletin* 80(8): 1471-1480.

f. Scholl, D.W., H.G. Greene, W.O. Addicott, W.R. Evitt, R.L. Pierce, S.H. Mamay, M.S. Marlow. 1969. Adak "Paleozoic" site, Aleutians—in fact of Eocene age [abs.]. *American Association of Petroleum Geologists Bulletin* 53(2): 459.

### 1970

a. Addicott, W.O. 1970. Biogeographical sketch of Leo Hertlein. *The Nautilus* 84(2): 37-41.

b. Addicott, W.O. 1970. Bibliography of Leo George Hertlein for the period of 1925 to 1970. *The Nautilus* 84(2): 43-52.

c. Addicott, W.O. 1970. Latitudinal gradients in Tertiary molluscan faunas of the Pacific coast. *Paleogeography, Palaeoclimatology, Palaeoecology* 8(4): 287-312.

d. Addicott, W.O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. U.S. Geological Survey Professional Paper 642: 1-174. <https://pubs.usgs.gov/pp/0642/report.pdf>

e. Addicott, W.O. 1970. Tertiary climatic change in San Joaquin Basin, California — evidence from shallow-water mollusks [abs.]. *American Association of Petroleum Geologists Bulletin* 54(3): 561.

f. Addicott, W.O. 1970. Tertiary paleoclimatic trends in the San Joaquin Basin, California. U.S. Geological Survey Professional Paper 644D: D1-D19.

g. Addicott, W.O. 1970. Additional remarks on studies of Cenozoic marine mollusks of the Pacific Coast. *The Veliger* 13(1): 110.

h. Addicott, W.O. 1970. Paleoclimatic history of the northeastern Pacific margin — a paleontologic application of modern molluscan zoogeographic data [abs.]. *The Echo, Western Society of Malacologists, Annual meeting, Stanford Calif.*: 15-16.

i. Musuda, K., and Addicott, W.O. 1970. On *Pecten (Amusium) condoni* Hertlein from the west coast of North America. *The Veliger* 13(2): 153-156.

### 1971

a. Addicott, W.O. 1971. Some Paleogene mud pectens of the genus *Propeamussium* from Alaska and California. *The Veliger* 13(3): 226-230.

b. Addicott, W.O. 1971. Tertiary marine mollusks of Alaska: an annotated bibliography. U.S. Geological Survey Bulletin 1343: 1-30.

c. Addicott, W.O. 1971. Some trends in Neogene marine molluscan paleontology on the west coast of North America. *Abstracts with Program, Geological Society of America* 3(2): 70.

### 1972

a. Addicott, W.O. 1972. Clark's Tertiary molluscan types from the Yakataga District, Gulf of Alaska. U.S. Geological Survey Professional Paper 750C: C18-C33.

b. Addicott, W.O. 1972. Neogene molluscan paleontology along the west coast of North America, 1840-1969 — trends and status. *Journal of Paleontology* 46(5): 627-636.

c. Addicott, W.O. 1972. Provincial middle and late Tertiary molluscan stages, Temblor Range, California. Pp. 1-26 [in:] *Proceedings of the Pacific Coast Miocene biostratigraphic symposium*. Pacific Section, S.E.P.M., Bakersfield. 364 pp.

d. Addicott, W.O., and G. Plafker. 1972. Paleocene mollusks from the Gulf of Alaska Tertiary province — a significant new occurrence on the North Pacific Rim. U.S. Geological Survey Professional Paper 750B: B48-B52.

### 1973

a. Addicott, W.O. 1973. A historical resume of research in Neogene marine molluscan paleontology and biostratigraphy in western North America. *Science Reports of the Tohoku University. Series 2: Geology — Tohoku Daigaku Rika Hokoku. Dai 2: Shu Chishitsugaku* 6(6): 7-14.

b. Addicott, W.O. 1973. Neogene marine mollusks of the Pacific coast of North America — an annotated bibliography, 1797-1969 — a compilation of reports for the period 1797-1969 dealing with marine mollusks of Miocene and Pliocene age. U.S. Geological Survey Bulletin 1362: 1-201.

c. Addicott, W.O. 1973. Oligocene molluscan biostratigraphy and paleontology of the lower part of the type Temblor Formation, California. U.S. Geological Survey Professional Paper 791: 1-48.

d. Addicott, W.O. 1973. Oligocene and Miocene molluscan stages, Temblor Range, California [abs.]. *American Association of Petroleum Geologists Bulletin* 57(2): 429.

e. Addicott, W.O. 1973. Giant Neogene pectinids of eastern North Pacific — chronostratigraphic and zoogeographic significance [abs.]. *American Association of Petroleum Geologists Bulletin* 57(4): 766.

f. Addicott, W.O., and J.S. Galehouse. 1973. Pliocene marine fossils in the Paso Robles Formation, California. U.S. Geological Survey Journal of Research 1(5): 509-514.

g. Bartow, J.A., A.M. Sarna-Wojcicki, W.O. Addicott, and K.R. Lajoie. 1973. Correlation of marine and continental Pliocene deposits in northern California

by tephrochronology [abs.]. American Association of Petroleum Geologists Bulletin 57(4): 769.

h. Galehouse, J.S., and W.O. Addicott. 1973. Paleo-geographic significance of Pliocene marine invertebrates from the Paso Robles Formation, southern Coast Ranges, California [abs.]. Abstracts with Programs, Geological Society of America 5(1): 46–47.

i. Nilsen, T. H., T.W. Dibblee, Jr., and W.O. Addicott. 1973. Lower and middle Tertiary stratigraphic units of the San Emigdio and western Tehachapi Mountains, California. U.S. Geological Survey Bulletin 1372H: 1–23.

**1974**

a. Addicott, W.O. 1974. Recognition and distribution of *Mytilus condoni* Dall, a unique Pliocene and Pleistocene bivalve from the Pacific Coast. The Veliger 16(40): 354–348.

b. Addicott, W.O. 1974. Giant Pectinids of the eastern North Pacific margin: significance in Neogene zoogeography and chronostratigraphy. Journal of Paleontology 48(1): 180–194.

c. Addicott, W.O., and H.G. Greene. 1974. Zoogeographic significance of a late Quaternary occurrence of the bivalve *Astarte* off the central California coast. The Veliger 16(3): 249–252.

**1975**

a. Addicott, W.O. 1975. Early Miocene age of the Clallam Formation, western Washington [abs.]. U.S. Geological Survey Bulletin 1405A: A26.

b. Addicott, W.O. 1975. Miocene biostratigraphy, western Washington, in Paleontology—Cenozoic of the United States [abs.]. U.S. Geological Survey Professional Paper 975: 176.

c. Addicott, W.O. 1975. Provincial age and correlation of the Clallam Formation, northwestern Washington [abs.]. Abstracts with Programs, Geological Society of America 7(3): 289.

d. Snavely, Jr., P.D., N.S. MacLeod, W.W. Rau, W.O. Addicott, and J.E. Pear. 1975. Alsea Formation – an Oligocene marine sedimentary sequence in the Oregon Coast Range. U.S. Geological Survey Bulletin 1395F: 1–21.

**1976**

a. Addicott, W.O. 1976. Molluscan paleontology of the lower Miocene Clallam Formation, northwestern Washington. U.S. Geological Survey Professional Paper 976: 1–44.

b. Addicott, W.O. 1976. New molluscan assemblages from the upper member of the Twin River Formation, western Washington: significance in Neogene chronostratigraphy. U.S. Geological Survey Journal of Research 4(4): 437–447.

c. Addicott, W.O. 1976. Neogene molluscan stages of Oregon and Washington. Pp. 95–115, in A.E. Fritsche, H. TerBest, Jr., and W.W. Wornardt [in:] Neogene Symposium. Pacific Section, S.E.P.M., San Francisco. 160 pp.

d. Addicott, W.O. 1976. On the significance of the bivalve *Acila gettysburgensis* (Reagan) in middle Tertiary chronostratigraphy of the Pacific Coast. The Veliger 19(2): 121–124.

e. Addicott, W.O., and P.D. Snavely, Jr. 1976. Reconnaissance of mollusk-bearing Neogene rocks, Almeria Province, eastern Andalusia, Spain [abs.]. Western Society of Malacologists, Annual Report 9: 49–50.

f. Allison, R.C., and W.O. Addicott. 1976. The north Pacific Miocene record of *Mytilus* (*Plicatomytilus*) a new subgenus of *Bivalvia*. U.S. Geological Survey Professional Paper 962: 1–22.

g. Plafker, G., and W.O. Addicott. 1976. Glaciomarine deposits of Miocene through Holocene age in the Yakataga Formation along the Gulf of Alaska margin, Alaska. U.S. Geological Survey Open-File Report 76-84: 1–36.

h. Plafker, G., and W.O. Addicott. 1976. Marine glacial deposits of Miocene through Holocene age along the Gulf of Alaska margin. Pp. 1–23 [in:] T.P. Miller, Recent and ancient sedimentary environments in Alaska. Alaska Geological Society, Anchorage 313 pp.

**1977**

a. Addicott, W.O. 1977. Neogene chronostratigraphy of nearshore marine basins of the eastern north Pacific. Proceedings of the First International Congress on Pacific Neogene Stratigraphy, Science Council, Japan. Tokyo: 151–175.

b. Addicott, W.O. 1977. Significance of pectinids in Tertiary biochronology of the Pacific Northwest States [abs.]. Abstracts with Programs, Geological Society of America 9(7): 874.

c. Addicott, W.O., P.D. Snavely, Jr., D. Bukry, and R.Z. Poore. 1977. Neogene stratigraphy and paleontology of southern Almeria Province, Spain: an overview. U.S. Geological Survey Open-File Report 77-716: 1–69.

d. Wehmiller, J.F., K.R. Lajoie, K.A. Kvenvolden, E. Peterson, D.F. Belknap, G.L. Kennedy, W.O. Addicott, J.G. Vedder, and R.W. Wright. 1977. Correlation and chronology of Pacific coast marine terrace deposits of continental United States by fossil amino acid stereochemistry – technique evaluation, relative ages, kinetic model ages, and geologic implications. U.S. Geological Survey Open-File Report 77-680: 1–196.

**1978**

a. Addicott, W.O. 1978. Late Miocene mollusks from the Queen Charlotte Islands, British Columbia, Canada. U.S. Geological Survey Journal of Research 6(5): 677–690.

b. Addicott, W.O. 1978. Marine paleogeography and paleontology of the Salinas basin during the latest

part of the Miocene with notes on macrofossils from near San Lucas, California. Pp. 83-90 [in:] Addicott, W.O., Neogene biostratigraphy of selected areas in the California Coast Ranges. U.S. Geological Survey Open-File Report 78-446 109 pp.

c. Addicott, W.O. (ed.). 1978. Neogene biostratigraphy of selected areas in the California Coast Ranges. U.S. Geological Survey Open-File Report 78-446:1-109.

d. Addicott, W.O. 1978. Notes on the geology of Point Lobos State Reserve, Monterey County, California. Pp. 91-96 [in:] Addicott, W.O., Neogene biostratigraphy of selected areas in the California Coast Ranges. U.S. Geological Survey Open-File Report 78-446 109 pp..

e. Addicott, W.O. 1978. Pectinids as biochronologic indices in the Neogene of the eastern North Pacific. Pp. 11-23 [in:] Proceedings of the second working group meeting biostratigraphic datum-planes of the Pacific Neogene. IGCP Project 114. Geological Research and Development Centre (Bandung, Indonesia), Special Publication 1 364 pp.

f. Addicott, W.O. 1978. Revision of the age of the Pancho Rico Formation, central Coast Ranges, California. U.S. Geological Survey Bulletin 1457A: 88-89.

g. Addicott, W.O., J.A. Barron, and J.W. Miller. 1978. Marine late Neogene sequence near Santa Cruz, California. Pp. 97-109 [in:] Addicott, W.O., Neogene biostratigraphy of selected areas in the California Coast Ranges. U.S. Geological Survey Open-File Report 78-446 109 pp.

h. Addicott, W.O., R.Z. Poore, J.A. Barron, H.D. Gower, and K. McDougall. 1978. Neogene biostratigraphy of the Indian Creek-Shell Creek area, northern La Panza Range, California. Pp. 11-38 [in:] Addicott, W.O., Neogene biostratigraphy of selected areas in the California Coast Ranges. U.S. Geological Survey Open-File Report 78-446 109 pp. [also available in Blake, G.H., 1980, Pacific Section, S.E.P.M 11-38].

i. Addicott, W.O., P.D. Snavely, Jr., D. Bukry, and R.Z. Poore., 1978. Neogene stratigraphy and paleontology of southern Almeria Province, Spain; an overview. U.S. Geological Survey Bulletin 1454: 1-49.

j. Addicott, W.O., G.R. Winkler, and G. Plafker. 1978. Preliminary megafossil biostratigraphy and correlations of selected stratigraphic sections in the Gulf of Alaska Tertiary province. U.S. Geological Survey Open-File Report 78-491 2 oversized sheets.

k. Armstrong, A.K., P.D. Snavely, Jr., and W.O. Addicott. 1978. Porosity evolution, late Miocene reefs, Almeria Province, southern Spain. U.S. Geological Survey Open-File Report 78-940: 1-20.

**1979**

a. Addicott, W.O. 1979. Oligocene molluscan biostratigraphy of the Indians, Santa Lucia Range, central California. Pp. 45-49 [in:] S.A. Graham, Tertiary and Quaternary geology of the Salinas Valley and Santa Lucia Range, Monterey County, California. Pacific Coast Paleogeography Field Guide 4 (Pacific Section, S.E.P.M.) 148 pp.

b. Addicott, W.O. 1979. The marine Cenozoic of the Pacific Coast states; an overview of the growth and development of biostratigraphic research. Pp. 325 [in:] J.M. Armentrout, M.R. Cole, and H. TerBest, Jr., Cenozoic paleogeography of the western United States: Pacific Coast Paleogeography Symposium (Pacific Section, S.E.P.M, Los Angeles, CA) 335 pp.

c. Addicott, W.O., P.D. Snavely, Jr., R.Z. Poore, and D. Bukry. 1979. La secuencia Neógena marina de los Campos de Dalias y de Nijar (Almeria). Estudios geológicos 35(1/2):609-631.

d. Armentrout, J.M., W.O. Addicott, J.A. Barron, and K. McDougall. 1979. Pacific Coast Neogene correlations; a progress report [abs.]. Abstracts with Programs, Geological Society of America 11(7): 381.

e. Clark, J.C., E.E. Brabb, and W.O. Addicott. 1979. Tertiary paleontology and stratigraphy of the central Santa Cruz Mountains, California coast ranges. Guidebook for Geological Society of America, Cordilleran Section, 75<sup>th</sup> annual meeting, April 1979: 23.

**1980**

a. Addicott, W.O. 1980. Biostratigraphy of the marine Neogene sequence at Cape Blanco, southwestern Oregon. U.S. Geological Survey Professional Paper 774G: 1-20.

b. Addicott, W.O. 1980. Biostratigraphy of the marine Miocene sequence at Cape Blanco, southwest Oregon [abs.]. Abstracts with Programs, Geological Society of America 12(3): 93.

c. Addicott, W.O. 1980. Highlights in the 130-year history of marine Cenozoic stratigraphic paleontology on the Pacific Coast of North America. Pp. 1-19 [in:] H. Igo, Professor Saburo Kanno Memorial Volume, Tsukuba University Publications 177 pp.

d. Addicott, W.O. 1980. Miocene stratigraphy and fossils, Cape Blanco, Oregon. Oregon Geology 42(5): 87-97.

e. Addicott, W.O. 1980. Status of the circum-Pacific map project: a summary of the Circum-Pacific map project meeting in Menlo Park, California, May 6-8, 1980. U.S. Geological Survey Open-File Report 80-1059: 1-77.

f. Addicott, W.O. 1980. Project 114, biostratigraphic datum-planes of the Pacific Neogene. U. S. contributions to the International Geological Correlation Program; a record of the activities and scientific contributions of United States participants, 1974-1979: 15-17.

g. Addicott, W.O., and R.Z. Poore. 1980. Paleogene/Neogene boundary in western North American sequences [abs.]: International Geological Congress, Abstracts—Congrès Géologique Internationale, Résumés 26(1): 194.

h. Addicott, W.O., and R.Z. Poore. 1980. The Paleogene–Neogene boundary in eastern North Pacific marine sequences [abs.]. Abstracts of Papers–Pacific Science Association, XIV Pacific Science Congress 2: 5–6.

i. Armstrong, A.K., P.D. Snavely, and W.O. Addicott. 1980. Porosity evolution of upper Miocene reefs, Almeria Province, southern Spain. American Association of Petroleum Geologists Bulletin 64(2): 188–208.

j. Reinemund, J.A., W.O. Addicott, and P.W. Richards. 1980. Circum–Pacific Map Project [abs.]. U.S. Geological Survey Professional Paper 1175: 335.

k. Stanley, S.M., W.O. Addicott and K. Chinzei. 1980. Lyellian curves in paleontology: possibilities and limitations. Geology 8(9): 422–426.

### 1981

a. Addicott, W.O. 1981. Brief history of Cenozoic marine biostratigraphy of the Pacific Northwest. Pp. 3–16 [in:] J.M. Armentrout Pacific Northwest Cenozoic Biostratigraphy. Geological Society of America, Special Paper 184 172 pp.

b. Addicott, W.O. 1981. Significance of pectinids in Tertiary biochronology of the Pacific Northwest. Pp. 17–38 [in:] J.M. Armentrout Pacific Northwest Cenozoic Biostratigraphy. Geological Society of America, Special Paper 184 172 pp.

c. Addicott, W.O. 1981. Mapping half the world; Circum–Pacific map project; 7<sup>th</sup> annual meeting, May 27–30, 1981, Menlo Park, California, U.S.A. Episodes 1981(2): 48–49.

d. Nolan, T.B., J.A. Reinemund, P.W. Guild, P.L. Bateman, A.L. Clark, J.R. Hein, W.D. Carter, W.D., W.O. Addicott, R.G. Coleman, G.K. Czamanske, J.E. Gair, R.B. Numan, G.M. Richmond, and R.P. Sheidon. 1981. International Geological Correlation Program. U.S. Geological Survey Professional Paper 1275: 277–278.

e. Poore, R.S., J.A. Barron, and W.O. Addicott. 1981. Biochronology of the northern Pacific Miocene. Pp. 91–97 [in:] N. Ikebe, M. Chiji, R. Tsuchi, Y. Morozumi, T. Kawata, Proceedings of IGCP 114 international workshop on Pacific Neogene biostratigraphy. 6th International working group meeting, Osaka, Japan, Nov. 25–29, 1981 142 pp.

### 1982

Reinemund, J.A., and W.O. Addicott. 1982. Circum–Pacific map project: framework for international resources assessment [abs.]. American Association of Petroleum Geologists Bulletin 66(7): 982.

### 1985

Addicott, W.O., coordinator. 1985. Manganese nodules, seafloor sediment, and sedimentation rates of the Circum–Pacific region/Circum–Pacific Council for Energy and Mineral Resources, Circum Pacific Map

Project. American Association of Petroleum Geologists: oversize map, scale 1:17,000,000.

### 1987

Moore, E.J., and W.O. Addicott. 1987. The Miocene Pillarian and Newportian (Molluscan) stages of Washington and Oregon and their usefulness in correlations from Alaska to California. U.S. Geological Survey Bulletin 1664: 1–13.

### 1988

Addicott, W.O., and Gryc, G. 1988. Scope and status of the Circum–Pacific map project: a programmatic overview including a resume of project activities during 1986 and 1987. U.S. Geological Survey Open-File Report 88-215: 1–110.

### ACKNOWLEDGMENTS

Many people are thanked for sharing their memories of Warren including Gene Coan, George Kennedy, Lindsey Groves, Robert McLaughlin, Ellen Moore, Andrei Sarna-Wojcicki, Judy Terry Smith, Richard Squires, Carol Stadum, Richard Stanley, Paul Valentich-Scott, and John Wehmiller. Special thanks are given to Eric Addicott, Warren's son, who shared the picture of Warren and of growing up with him. Ashley Dineen (University of California, Museum of Paleontology) is thanked for providing down information about Warren's time at UCMP. Also thanked are Mary McGann and Richard Stanley (USGS) for their helpful reviews.

### OTHER LITERATURE CITED

Addicott, W.O. 1967d. Boutoniere camellias, 1962–1966: comments and ratings. The Camellia Review 28(3): 1–44 (January 1967) [http://socalcamelliasociety.org/wp-content/uploads/Camellia\\_Review/Vol\\_28/CR-0167.pdf](http://socalcamelliasociety.org/wp-content/uploads/Camellia_Review/Vol_28/CR-0167.pdf)

Addicott, W.O., R.Z. Poore, J.A. Barron, H.D. Gower, and K. McDougall. 1980. Neogene biostratigraphy of the Indian Creek–Shell Creek area, northern La Panza Range, California. Pp. 11–38 [in:] G.H. Blake. 1980. Neogene biostratigraphy of the northern La Panza Range San Luis Obispo County, California. Pacific Section, SEPM (Society for Sedimentary Geology). 44 pp.

Adegoke, O.S. 1969. Stratigraphy and paleontology of the marine Neogene formations of the Coalinga region, California. University of California Publications in Geological Sciences 80: 1–269.

Carson, C.M. 1926. New molluscan species from the California Pliocene. Bulletin of the Southern California Academy of Sciences 25(2): 49–62.

Clark, B.L. 1932. Fauna of the Poul and Yakataga formations (upper Oligocene) of southern Alaska. Geological Society of America Bulletin 43(3): 797–846.

Clarke, M.R., and J.E. Fitch. 1979. Fossil statoliths of Cenozoic teuthoid Cephalopoda of North America. Palaeontology 22: 498–400.

Emerson, W.K. 1957. Three new Tertiary scaphopods, with a review of the extinct western North American Siphonodontaliidae. Journal of Paleontology 31(5): 985–991.

Hickman, C.S. 2009. Architects of the Berkeley legacy of Cenozoic molluscan paleontology - part II. UCMP (University of California Museum of Paleontology) News, February 2009 [https://ucmp.berkeley.edu/about/ucmpnews/09\\_02/legacy09\\_02.php](https://ucmp.berkeley.edu/about/ucmpnews/09_02/legacy09_02.php)

Kafanov, A.I., 1986[1985], Dva novykh vida *Mytilus* (Bivalvia, Mytilidae) iz miotsenovykh otlozheniy Kamchatki i tikhookeanskogo poberezh'ya Severnoy Ameriki [Two new species of *Mytilus* (Bivalvia, Mytilidae) from Miocene deposits of Kamchatka and Pacific coast of North America]. Pp. 107–109 [in:] Kafanov, A.I. 1986[1985]. Paleogen-Neogenovye dvustvorchatye mollyuski Dal'nego Vostoka i vostochnogo Paratetisa [Paleogene and Neogene bivalve mollusks of Far East and East Parathetys]. Far East science Center, Academy of Sciences of the USSR, Vladivostok 132 pp. (in Russian; translation in brackets).

Kanno, S. 1971. Tertiary molluscan fauna from the Yakataga District and adjacent areas of southern Alaska. Palaeontological Society of Japan Special Paper 16: 1 –154.

Moore, E.J. 1984. Molluscan paleontology and biostratigraphy of the lower Miocene upper part of the Lincoln Creek Formation in southwestern Washington, USA. Natural History Museum of Los Angeles County, Contributions in Science 351: 1 –42.

Southern California Camellia Society. 1964. Show Results. The Camellia Review 25(6): 1–44 (May 1964.) [http://socalcamelliasociety.org/wp-content/uploads/Camellia\\_Review/Vol\\_25/CR-0564.pdf](http://socalcamelliasociety.org/wp-content/uploads/Camellia_Review/Vol_25/CR-0564.pdf)

Southern California Camellia Society. 1968. Show Results. The Camellia Review 29(6): 1–36 (May 1964.) [http://socalcamelliasociety.org/wp-content/uploads/Camellia\\_Review/Vol\\_29/CR-0568.pdf](http://socalcamelliasociety.org/wp-content/uploads/Camellia_Review/Vol_29/CR-0568.pdf)

Nikas, A.J., III. 1977. Description of a new bivalve of the genus *Macoma* from the Pliocene of central California. The Veliger 19(4): 434 –437.

Zinsmeister, W.J. 1983. New late Paleocene molluscs from the Simi Hills, Ventura County, California. Journal of Paleontology 57(6): 1282 –1303.

Zullo, V.A. 1979. Thoracican Cirripedia of the lower Pliocene Pancho Rico Formation, Salinas Valley, Monterey County, California. Natural History Museum of Los Angeles County, Contributions to Science 303: 1 –13.

# Six new species of *Paciocinebrina* (Gastropoda: Muricidae: Ocenebrinae) from the northeast Pacific

Shawn G. Wiedrick<sup>1</sup>

Natural History Museum of Los Angeles County  
900 Exposition Blvd.  
Los Angeles, California, 90007, USA  
shawnwiedrick@hotmail.com

Roland Houart<sup>2</sup>

Royal Belgian Institute of Natural Sciences, Rue Vautier 29,  
1000 Brussels, Belgium and Institute of Systematics, Evolution,  
Biodiversity (ISYEB)  
and  
Muséum national d'Histoire naturelle (MNHN), CNRS, SU,  
EPHE, UA, CP 51, 57 rue Cuvier, 75005 Paris, France  
roland.houart@skynet.be

## ABSTRACT

The western North American genus, *Paciocinebrina* Houart, Vermeij, and Wiedrick 2019, is both impressively speciose and phenotypically plastic, challenging the views of both lumpers and splitters. A recent study has revealed that the northeastern Pacific species of *Paciocinebrina* are distinct from the European type species, *Ocinebrina aciculata* (Lamarck, 1822) and other eastern Atlantic species, including *Ocenebra* Gray, 1847. Based on newly collected specimens and material already available, mostly from California, a spiral morphology comparison of six new species are herein described, including habitat and distribution records.

*Additional Keywords:* Gastropoda, Muricidae, Ocenebrinae, *Paciocinebrina*, new species, northeastern Pacific Ocean

## INTRODUCTION

The predatory snail genus *Paciocinebrina* Houart, Vermeij, and Wiedrick, 2019 has long been a grouping of temperate snails chiefly restricted to the northeast Pacific and similar in appearance to northeastern Atlantic and Mediterranean species of *Ocinebrina* Jousseaume, 1880. Molecular studies (Barco et al., 2017) support these genera as distinct lineages, both having radiations of diversity. Houart et al. (2019) used morphological and biogeographic comparisons to provide a faunal list and to describe several new species from the southern range of *Paciocinebrina*. *Paciocinebrina* is one of about 33 recognized genera within the muricid subfamily Ocenebrinae Cossmann, 1903 (Molluscabase eds., 2020). Voucher material examined range from intertidal to subtidal (to 686 m) habitats, and were reported from as far north as the Kenai Peninsula, Kenai-Cook County, Alaska (59° N) and as far south as Bahía Magdalena, Baja California Sur,

Mexico (24° N). Assuming that the LACM collections examined accurately reflect distributional patterns, these snails are much more abundant in the northern portion of the range but are still present at moderate densities south of San Luis Obispo County, California.

The diversity of this group has long been debated, highlighted by the conflicted views of Radwin and D'Attilio (1976) and Fair (1976). Shell and radular morphology have been the basis of *Paciocinebrina* descriptions (Radwin and D'Attilio, 1971; 1976), with morphological characters having a historical perspective, embraced by malacologists in the diagnosis of molluscan species and higher taxa in systematic studies (Ponder and Lindberg, 1997).

The reproductive life histories of this group are poorly understood and known from very few studies (Merle et al., 2011: 23). Paleobiologists (Jablonski and Lutz, 1983) have found that morphological features in the protoconch sculpture of marine benthic gastropods are a result of their mode of development (Bouchet and Strong, 2010: 65; Merle et al., 2011: 23). The use of this feature to determine species delineation, biodiversity, and life history patterns has been broadly used for neogastropods (Shuto, 1974; Bouchet, 1990), including studies on muricids (Radwin and D'Attilio, 1976; D'Attilio, 1980; 1981; Myers and D'Attilio, 1986; Merle et al., 2011: 17, 23) and conoideans (Powell, 1966: 6; Bouchet, 1990). The uniform possession of paucispiral protoconchs in eastern Pacific *Paciocinebrina* species was noted by McLean (1996: 80) and indicates that the mode of reproduction across the taxon is by intracapsular development. Hansen (1980), Jablonski and Lutz (1983), and Jablonski (1986) found higher speciation and extinction rates in this mode of development, which seems to parallel the radiation and fossil record of this group (Marshall et al., 2012; Nützel, 2014). Fluctuating sea level and temperature changes likely contributed to higher periods of diversification, whether in warm periods (Mayhew et al., 2012) or cold periods (Davis et al., 2016), as reflected in the Neogene

<sup>1</sup> Museum Associate

<sup>2</sup> Research Associate at both institutions listed

and Quaternary fossil record of California. Modes of larval dispersal may have been under selection by the strong currents seen in the eastern Pacific, a model discussed by Brown (2014).

Several contributing factors are likely the cause of species within this genus to inhabit rocky substrate, whether intertidal or subtidal. Ecological and physiological factors such as reproduction, feeding, and ecological niches are likely influenced by habitat selection by these gastropods. Abbott (1968: 126) illustrated western Atlantic muricid egg capsules, which appear to be similar in appearance to northeastern Pacific *Paciocenebrina* species. Laboratory studies by Spight et al. (1974: 234) detailed egg capsule laying on rocks by *Paciocenebrina interfossa* (Carpenter, 1864), with Griffith (1967: 69) noting some eastern Pacific muricids known to guard eggs during incubation. This reproductive process appears to limit connectivity between populations, as long spanning, intertidal and subtidal sandy shorelines tend to isolate rocky reefs in the eastern Pacific, which could restrict migration between these populations, isolating them to rocky habitats. Diet, feeding preference, and food abundance likely play a role in habitat selection. Species within this group are carnivorous and feed by means of radula and an accessory boring organ, which in combination, are capable of drilling through a prey's hard flesh or exoskeleton (Vermeij, 1993: 105, 108; McLean, 2007: 740; Bertsch and Rosas, 2016: 216–217). The preferred diet of *Paciocenebrina* species is primarily comprised of sessile barnacles, mollusks, and other invertebrates restricted to rocky habitats.

*Paciocenebrina* species have been reported as feeding or associated with the mantle of the gumboot chiton, *Cryptochiton stelleri* (Middendorff, 1846) (Talmadge, 1975; Abbott and Haderlie in Morris et al., 1980: 277), barnacles (Rice, 1971: 48; Abbott and Haderlie, 1980: 277; Palmer, 1988; McLean, 2007: 740; McLean, 1996: 78; Bertsch and Rosas, 2016: 216; Merle et al., 2011: 24), limpets (Palmer, 1988; Bertsch and Rosas, 2016: 216), bivalves (Palmer, 1988; McLean, 2007: 740; McLean, 1996: 78; Merle et al., 2011: 24), other mollusks (Palmer, 1988; Abbott and Haderlie, 1980: 277; Merle et al., 2011: 24) and the shelled polychaete worm, *Spirorbis* (Palmer, 1988: 192).

New species descriptions are based on the analysis of type material from the California Academy of Sciences (CASIZ), Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDNHM), National Museum of Natural History, Smithsonian Institution (USNM), University of California, Museum of Paleontology (UCMP), several private collections, and the collection of subtidal and intertidal specimens ranging from Devil's Gate, Humboldt Co. (40°N) to Laguna Beach, Orange Co., California (33°N). A revision of *Paciocenebrina* is presented in Wiedrick (thesis) including the chresonymy, synonymy, biodiversity, biogeography, and ecology of known nominal taxa based on existing literature, the aforementioned specimens, and molecular data.

## MATERIALS AND METHODS

### INSTITUTIONAL ABBREVIATIONS

CASIZ: California Academy of Sciences, Invertebrate Zoology, San Francisco, California, U.S.A

LACM: Natural History Museum of Los Angeles County, Malacology Department, California, U.S.A.

NHMUK: Natural History Museum of the United Kingdom, London, England, U.K.

SDNHM: San Diego Natural History Museum, San Diego, California, U.S.A.

SGW: collection of Shawn G. Wiedrick

UCMP: University of California, Museum of Paleontology, Berkeley, California, U.S.A.

USNM: National Museum of National History, Smithsonian Institution, Washington, D. C., U.S.A.

ZIN: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia

### SPIRAL MORPHOLOGY ABBREVIATIONS

Terminology used to describe the spiral cords and the internal denticles of the outer lip (based on Merle, 1999; 2001; 2005; Merle and Houart, 2003):

**ab:** abapical (or abapertural); **abis:** abapical infrasutural secondary cord (on subsutural ramp); **ABP:** abapertural primary cord on the siphonal canal; **abs:** abapertural secondary cord on the siphonal canal; **ad:** adapical (or adapertural); **adis:** adapical infrasutural secondary cord (on subsutural ramp); **ADP:** adapertural primary cord on the siphonal canal; **ads:** adapertural secondary cord on the siphonal canal; **IP:** infrasutural primary cord (primary cord on subsutural ramp); **MP:** median primary cord on the siphonal canal; **ms:** median secondary cord on the siphonal canal; **P:** primary cord; **P1:** shoulder cord; **P2–P6:** primary cords of the convex part of the teleoconch whorl; **s:** secondary cord; **s1–s6:** secondary cords of the convex part of the teleoconch whorl; **SP:** subsutural cord; **t:** tertiary cords; **D1–D6:** abapical denticles; **ID:** infrasutural denticle.

## RESULTS

### SYSTEMATICS

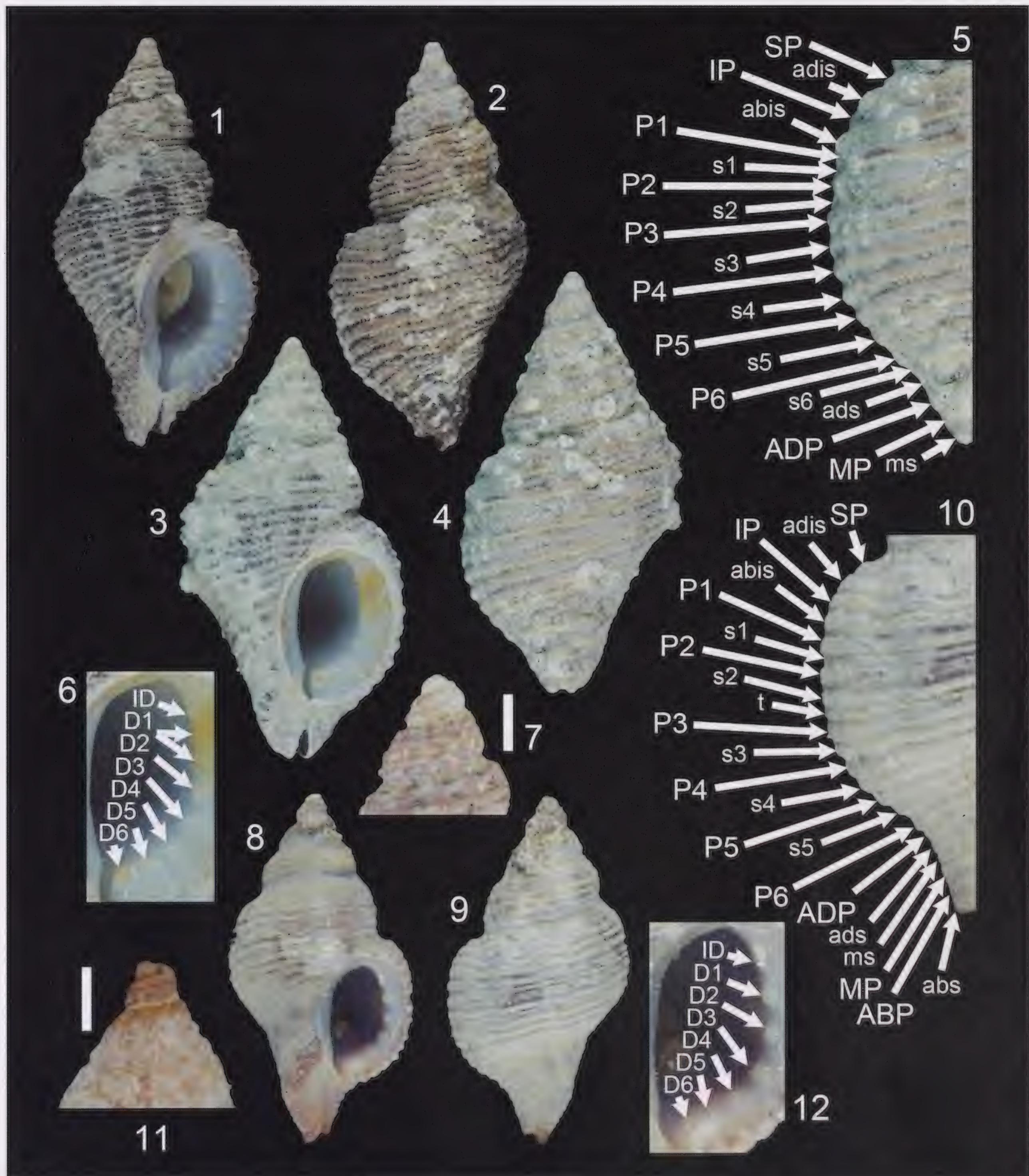
Muricidae Rafinesque, 1815  
Ocenebrinae Cossmann, 1903

### Genus *Paciocenebrina* Houart, Vermeij and Wiedrick, 2019

**Type Species:** *Tritonium (Fusus) luridum* Middendorff, 1848: 244, by original designation, Recent, Sitka, Alaska (Syntype, ZISP 62131).

**Remarks:** The complete faunal list and description was provided by Houart et al. (2019: 209–210). Additional new species are proposed below.

### *Paciocenebrina bormannae* new species (Figures 8–12)



**Figures 1-12.** *Paciocinebrina* species. **1-7.** *Paciocinebrina grandilurida* new species. **1-2.** Shelter Cove, California, intertidal on rock, length 26.2 mm, width 13.5 mm (SGW 115). **3-4.** Holotype, Shelter Cove, California, intertidal, length 27.0 mm, width 15.0 mm (LACM 3761). **5.** Spiral cords morphology. **6.** Apertural denticles morphology. **7.** Protoconch, scale bar: 1.0 mm (SGW 116). **8-12.** *Paciocinebrina bormannae* new species. **8-9.** Holotype, Cayucos, California, on rocks at low tide, length 22.4 mm, width 12.3 mm, (LACM 3760). **10.** Spiral cords morphology. **11.** Protoconch, scale bar: 1.0 mm (SGW 117). **12.** Apertural denticles morphology.

## CHRESONYMY

*Ocenebra lurida aspera*.—Smith and Gordon, 1948: 189.  
*Ocenebra lurida*.—Abbott and Haderlie, 1980: 277–278,  
 fig. 13.76.

*Ocinebrina foveolata*.—Liff-Grieff, 2006: 4, lower right  
 figures.

**Description:** Large for genus, holotype 22.4 mm in length, width 12.3 mm. Shell robust, thick, shape broad, elongate-ovate, spire angle variable, siphonal canal narrow, short, acutely tapered, color rustic brown, with dark brown incised lines between cords, aperture white, blue overtones, siphonal canal creamy tan. Protoconch bulbous with subtle carination, shoulder and median cord abruptly formed, converged by vertical ribs of first teleoconch whorl, clathrate in appearance, later cords strong, overriding ribs, fimbriations vaulted, close set, extremely fine and low profile in interspaces. First teleoconch whorl with P1, P2 spiral cords, second with P1 and P2 cords, starting IP and s1 cords, third whorl with IP, P1, s1, P2 cords, starting adis and s2 cords, fourth with adis, IP, P1, s1, P2, s2 cords, starting P3 cord, final whorl with SP, adis, IP, abis, P1, s1, P2, s2, t, P3, s3, P4, s4, P5, s5, P6, ADP, ads, ms, MP, ABP and abs spiral cords, nine faint axial ribs on final whorl. Apertural denticles morphology with ID and six primary denticles, ID denticle extremely indistinct, D1 denticle weak, D2–D4 denticles stronger, final denticles slightly weaker. Aperture elongate ovate, moderate in size, lip of aperture thick, edge sharp, strongly projecting, parietal wall weak posteriorly, thicker anteriorly of columellar wall, siphonal canal comparatively thin, tapered towards anterior end.

**Type Material:** Holotype LACM 3760, length 22.4 mm, width 12.3 mm.

**Type Locality:** Cayucos, San Luis Obispo County, California, (35°26'40" N, 120°56'42" W), on rocks at low tide.

**Other Material Examined:** Two specimens, 12.1–38.1 m, Carmel Submarine Canyon, north end San Jose Creek Beach, Monterey County, California (36°31'59" N, 121°55'59" W), collected by J.H. McLean, 1960–1964 [LACM 1960–24.105]; two specimens, Monterey, Monterey County, California [LACM 151093]; four specimens, intertidal on shale ledges, west of Cayucos Creek, San Luis Obispo County, California (35°26'48" N, 120°54'29" W), collected by P.I. LaFollette, 11 December 1977 [LACM 1977–112.48]; four specimens, Cayucos, San Luis Obispo County, California, collected by Bormann [LACM 72468]; one specimen, intertidal, Dinosaur Cave, Shell Beach, San Luis Obispo County, California (35°9'11" N, 120°40'36" W), collected by P.M. Oringer, 19 December 1968 [LACM 1968–48.23]; six specimens from Shell Beach, San Luis Obispo County, California (35°9'24" N, 120°40'36" W), intertidal on shale ledges, collected by J.H. McLean, 1961–1963 [LACM 1961–11.50]; six specimens, near Arroyo Grande, San Luis Obispo County, California [LACM 59600]; three specimens, San Luis Obispo County, California [LACM 59620]; one specimen, 3.2 km north of

Avalon, Santa Catalina Island, California Channel Ids., California (33°23'59" N, 118°22'0" W), collected by J.H. McLean, 29 April 1962 [LACM 1962–5.31].

**Distribution:** Carmel Submarine Canyon, Monterey Co., California (36°) to Avalon, Santa Catalina Island, California Channel Ids., California (33°N); primarily on low intertidal rocks, large rock overhangs and undersides of giant boulders, to 38.1 m.

**Remarks:** The spiral morphology of the initial whorl are identical (P1 and P2) to various other *Paciocinebrina* species, with distinct s2 cord in the second whorl of *P. bormannae*, third whorl with adis cord, a feature not seen in comparable species, fourth whorl similar to *Paciocinebrina munda* (Carpenter, 1864), with P3 cord absent in that species, final whorl of *P. bormannae* with SP, abis, s4, ads, ms, abs cords and s6 cord absent, all characters not seen in *P. munda* (Figures 56–59). Superficially similar to the more northern species, *P. grandilurida* new species, but is lighter in coloration, has a less acute spire, one additional axial rib on final whorl and a different spiral cord morphology with *P. bormannae* having an additional t cord after s2 and ABP, abs cords on final whorl (Figures 5, 10).

**Etymology:** Named in honor of the late Mary Bormann, a collector of various *Paciocinebrina* species, who also had a particular passion for this group of west coast muricids.

***Paciocinebrina grandilurida* new species**  
 (Figures 1–7)

**Description:** Shell large for genus, holotype length 27.0 mm, width 15.0 mm. Shape acute rhomboid, outer lip projecting, thick, spire acute, siphonal canal moderately long, color dark brown to black, interspaces lighter in appearance, canal face white, aperture interior often with blue overtone. Initial protoconch whorl low laying, bulbous, tabulation faint, shoulder and median cords well established, ribs becoming well developed, first teleoconch whorl with overriding spiral cords, further whorls forming large, thick, tightly set cords, final whorl surface heavily scabrous, especially between cords, obscurely clathrate. First teleoconch whorl with P1, P2 spiral cords, second with P1, P2 cords, starting IP cord, third whorl with IP, P1, P2, s2 cords, starting s1, s2 cords, fourth with IP, P1, s1, P2, s2 cords, starting adis, abis cords, final whorl with SP, adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, ads, ADP, MP, ms spiral cords, eight very faint, broadly spaced axial ribs on final whorl. Aperture elongate ovate, with ID, D1 split and five additional denticles, columellar lip wide, recessed into previous whorl, siphonal canal rather short, pseudoumbilicus faint.

**Type Material:** Holotype LACM 3761, length 27.0 mm, width 15.0 mm.

**Type Locality:** Shelter Cove, Humboldt County, California, (40°1'24" N, 124°4'24" W) on rocks at low tide.

**Other Material Examined:** 12 specimens, intertidal, near Machi Brothers Resort, Shelter Cove, Humboldt

County, California ( $40^{\circ}01'29''$  N,  $124^{\circ}04'00''$  W), collected by P. I. LaFollette, 19–20 July 1970 [LACM 70–70.40]; four specimens, intertidal on rocks, Van Damne State Park, Little River, Mendocino County, California ( $39^{\circ}17'42''$  N,  $123^{\circ}47'48''$  W), collected by J.H. McLean, 22 February 1964 [LACM 64–8.34]; two specimens, intertidal, Albion, Mendocino County, California ( $39^{\circ}14'30''$  N,  $123^{\circ}46'30''$  W), collected by J.H. McLean, 11 November 1962 [LACM 62–15.30]; two specimens, intertidal, 0.8 km south of Fort Ross, Sonoma County, California ( $38^{\circ}30'42''$  N,  $123^{\circ}13'59''$  W), collected by J.H. McLean, 28 December 1963 [LACM 63–57.23].

**Distribution:** Shelter Cove, Humboldt Co., California ( $40^{\circ}$ N) to Fort Ross, Sonoma Co., California ( $38^{\circ}$ N); low to mid intertidal zone, on rock reefs, undersurfaces of large boulders and on the girdle of the gumboot chiton, *Cyptochiton stelleri* (Middendorff, 1846).

**Remarks:** The first three whorls are identical to *Paciocinebrina munda* (P1, P2; IP, P1, P2; IP, P1, s1, P2, s2), with abis cord of fourth whorl absent in *P. munda*. See *P. bormannae* section for comparisons to this species. Talmadge (1975: 414), Abbott and Haderlie (1980) and McConaughey and McConaughey (1985: 358) reported the feeding of *Paciocinebrina lurida* (Figures 60–63) on the gumboot chiton, *Cyptochiton stelleri* (Middendorff, 1846), although field observations from Shelter Cove have exclusively been by the larger *P. grandilurida*, despite the mass presence of *P. lurida* at that locality.

**Etymology:** In reference to the large size and similarities to the smaller *Paciocinebrina lurida* (Middendorff, 1848), *grandi-* meaning grandiose, *lurida* in reference to that other species, gender feminine.

#### *Paciocinebrina mininterfossa* new species

(Figures 13–18)

##### CHRONSYNOMY

*Ocenebra interfossa*.—Rice, 1971: pl. 17, fig. 98.

**Type Material:** Holotype LACM 3762, length 13.1 mm, width 6.1 mm (*ex* SGW 114).

**Type Locality:** China Rock, Seventeen Mile Drive, Monterey County, California, ( $36^{\circ}36'10''$  N,  $121^{\circ}57'42''$  W), on rocks at low tide.

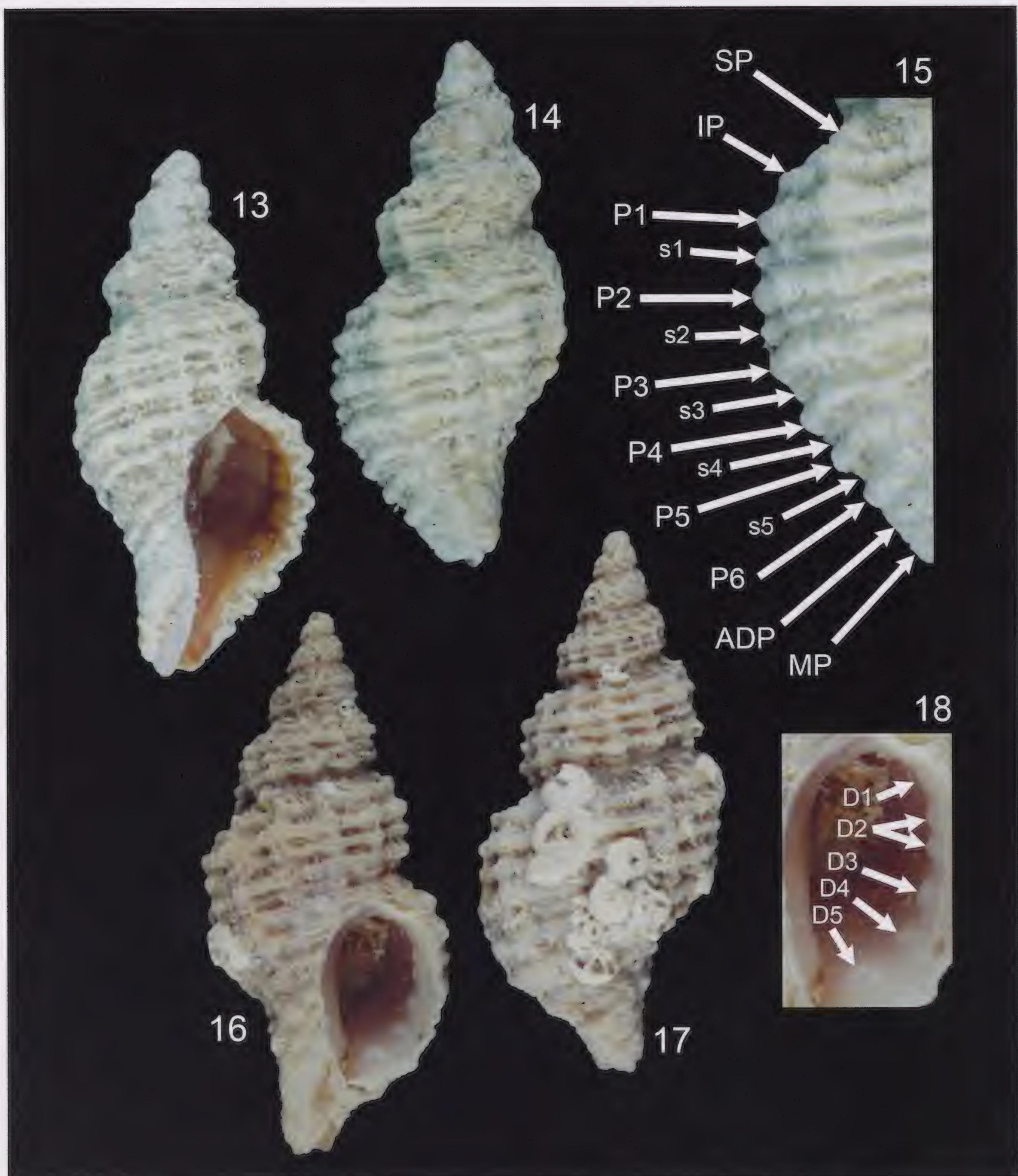
**Other Material Examined:** Five specimens, Crescent City, Del Norte County, California, collected by E. P. Chace [LACM 72475]; two specimens, 18 m, Isle of St. James, North Farallon Islands, California ( $37^{\circ}45'40''$  N,  $123^{\circ}5'57''$  W), collected by R.W. Schmieder, R/V CORDELL EXPLORER, 14 September 1991 [LACM 1991–177.19]; two specimens, intertidal on rocks, south side of Point Joe, Seventeen Mile Drive, Monterey County, California ( $36^{\circ}36'29''$  N,  $121^{\circ}57'29''$  W), collected by P.I. LaFollette, June 1962 [LACM 1962–43.4]; 10 specimens, intertidal, Pacific Grove, Monterey County, California ( $36^{\circ}37'22''$  N,  $121^{\circ}54'34''$  W), collected by J.H. McLean, 1959–1964

[LACM 1959–12.63]; one specimen, intertidal on *Phyllospadix* roots, Hopkins Marine Station, Pacific Grove, Monterey County, California ( $36^{\circ}37'30''$  N,  $121^{\circ}54'00''$  W), collected by J.H. McLean, 1 December 1962 [LACM 1962–16.17]; three specimens, Pacific Grove, Monterey County, California [LACM 151066].

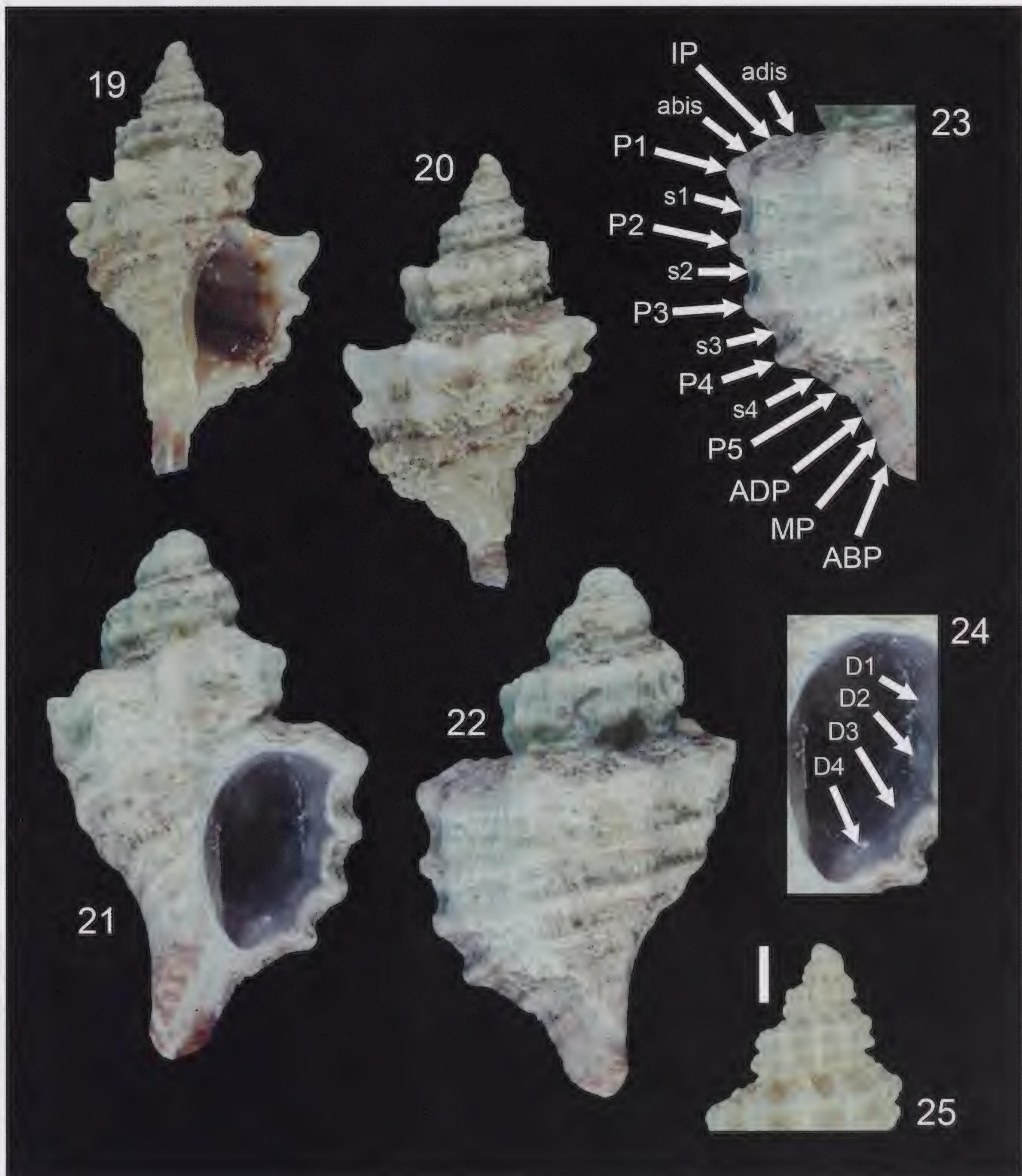
**Distribution:** Crescent City, Del Norte Co., California ( $41^{\circ}$ N) to China Rock, Seventeen Mile Drive, Monterey, Monterey Co., California ( $36^{\circ}$ N); primarily at low to mid-intertidal zones on rocks, near dense mats of purple algae, as noted on one LACM record from near the surfgrass, *Phyllospadix*, 1 subtidal lot at 18 m.

**Description:** Shell small for the genus, holotype length 13.1 mm, width 6.1 mm. Shell elongate, profile narrow, slenderly rhomboid, whorls ovate, tall, sutural indentations weak, size small, but robust, ribs subtle, scabrous sculpture of even width throughout entire length of shell, color dingy white, occasionally with light brown band on P2 cord below shoulder, outer lip of aperture dull white, columellar and parietal walls and interior flushed with purplish brown. Spire acute, protoconch bulbous, worn in nearly all specimens examined. Initial whorl somewhat flattened, wide spanning, half set into proceeding whorl, rotund, becoming shouldered by cord further into whorl than most other *Paciocinebrina* species. Median cord strong, slightly more projecting initially, becoming of equal strength and pseudo-clathrate, spiral cords becoming projected nodes at intersection of axial ribs. Shape of siphonal canal moderately small, tapering. First teleoconch whorl in holotype with P1, P2 cords, second with P1, P2 cords, starting IP cord, third with P1, P2 cords, starting, s1 cord, fourth whorl with IP, P1, s1, P2 cords, starting s2 cord, final whorl with SP, IP, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, ADP, MP spiral cords and eleven narrow, but widely spaced axial ribs. Aperture consistently with weak D1, D2 (split), D3, D4, D5 denticles, strongest centrally, split D2 denticles weak in small sized specimens. Aperture moderately sized, ovate, posterior end squarer in shape, lip heavily developed and thick at subsutural ramp on final varices, slightly slimmer at shoulder, thinning towards anterior end, parietal wall extremely thin at top, wider anteriorly, slightly thicker at columellar wall, terminated by a twist near anterior end.

**Remarks:** The initial three teleoconch whorls are identical to *Paciocinebrina minor* (Dall, 1919) (Figures 44–47), with *P. mininterfossa* having adis, abis, s1, s2, s3, s4, s5 and P6 cords on the fourth whorl, characters absent in *P. minor*. This species is very small compared to the similar appearing species, *P. interfossa* (Figures 64–67), of which many specimens have been haphazardly mixed into LACM lots labelled as such, a likely assumption is that workers simply presumed a juvenile state in this smaller species. Additionally, this taxon is a dingy white, not brown, has thicker and much looser sutural scabrocity and a different spiral morphology. A specimen figured by Rice (1971), and identified as *P. interfossa*, seems to match the holotype of this species and



**Figures 13-18.** *Paciocinebrina mininterfossa* new species. **13-14.** China Rock, California, on intertidal rock, length 12.7 mm, width 6.3 mm, (SGW 118). **15.** Spiral cords morphology. **16-17.** Holotype, China Rock, California, on intertidal rock, length 13.1 mm, width 6.1 mm, (LACM 3762). **18.** Apertural denticles morphology.



**Figures 19–25.** *Paciocinebrina murphyorum* new species. **19–20.** Shell Beach, California, length 9.6 mm, width 5.6 mm (SGW 119). **21–22.** Holotype, Jade Cove, California, on rock at 14.6 m, length 11.7 mm, width 7.2 mm, (LACM 3763). **23.** Spiral cords morphology. **24.** Apertural denticles morphology. **25.** Protoconch, scale bar: 1.0 mm (SGW 120).

is here included, despite Rice (1971) neglecting to provide a specific locality of the figured specimen. This species has been observed in the field as feeding on *Barleeia* species.

**Etymology:** Gender feminine in the nominative case, *mini-* meaning a miniature version of *P. interfossa*, meaning having ditches among itself, in reference to the sculpture of that species.

***Paciocenebrina murphyorum* new species**

(Figures 19-25)

CHRONOMY

*Ocenebra interfossa clathrata*.—Bormann, 1946: 39, pl. 4, fig. 1, 3.

**Description:** Shell small for genus, holotype length 11.7 mm, width 7.2 mm. Shape rhomboid, severely indented at whorl base, siphonal canal moderately long, narrow, whorls tabulate, sculpture clathrate, of thick intersecting cords and ribs, color chalky white with dark brown bands at suture to mid-subsutural ramp, and posteriorly before cords P3 through P4, aperture interior usually brown or brownish purple, parietal wall lighter in coloration, somewhat thin, twisted anteriorly. Initial protoconch whorl upward projecting, rapidly downward angled in shoulder cord, anteriorly tabulate, cords equal in strength, rectangularly clathrate at rib intersections, deep squarish pits on final whorl, early whorl growth lines faint, crissate scales tightly spaced on final whorl, less evident in pits. First two teleoconch whorls with P1, P2 cords, third with P1, P2 cords, starting P3 cord, fourth whorl with adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, ADP, MP, ABP spiral cords, nine strong, widely spaced axial ribs, projecting at shoulder on final whorl. Aperture somewhat small, ovate with D1-D4 denticles, outer lip projecting, lip thickened, parietal wall closely attached, narrow, siphonal canal long, spindle-like from basal indentation.

**Type Material:** Holotype LACM 3763, length 11.7 mm, width 7.2 mm.

**Type Locality:** Jade Cove, Big Sur, Monterey County, California, (35°54'46" N, 121°28'29" W), on rock at 14.6 m.

**Other Material Examined:** Two specimens, Roller Bay, intertidal rocks, Hope Island, Vancouver Island, Rupert District, British Columbia, Canada (50°55'36" N, 127°57'5" W), collected by J.H. McLean, 22 May 1963 [LACM 1963-31.22]; four specimens at 9-15 m, 100 m inshore of buoy at Point Delgado, Humboldt County, California (40°0'29" N, 124°04'00" W), collected by C.C. Swift, R/V SEARCHER, 29 July 1971 [LACM 1971-107.12]; one specimen at 0.3 m on rocks, northwest of Pico Creek, San Simeon Village, San Luis Obispo County, California (35°36'55" N, 121°9'4" W), collected by P.I. LaFollette, 8 August 2006 [LACM 2006-28.1]; three specimens, Cayucos, San Luis Obispo County, California, collected by R. and M. Bormann [LACM 72480]; six specimens, intertidal on shale ledges, Shell Beach, San Luis Obispo

County, California (35°9'24" N, 120°40'36" W), collected by J.H. McLean, 1961-1963 [LACM 1961-11.48]; 12 specimens, intertidal on shale ledges and boulder reef, 0.4 km northwest of South Point, Shell Beach, San Luis Obispo County, California (35°9'18" N, 120°40'29" W), collected by P.I. LaFollette, 10 December 1977 [LACM 77-111.44]; one specimen, intertidal, Avila Beach, San Luis Obispo County, California (35°10'59" N, 120°43'59" W), collected by P.M. Oringer, 28 July 1968 [LACM 1968-37.36]; two specimens, San Nicolas Island, California Channel Ids., California, MacGinitie collection, 17-19 July 1962 [LACM 59601].

**Distribution:** Hope Island, Vancouver Island, British Columbia (50° N) to San Nicolas Island, California Channel Ids., California (33° N); on and under intertidal rocks, in gravel, rarely at shallow subtidal depths to 14.6 m.

**Remarks:** The initial three whorls are identical to *Paciocenebrina minor*, with *P. murphyorum* having adis, abis, s1, s2, s3 and s4 spiral cords on fourth whorl, characters absent in *P. minor*. This species superficially resembles *P. atropurpurea* (Carpenter, 1865) but has a different morphology (Figures 52-55) than *P. murphyorum* (Figures 23-24). Bormann (1946: pl. 4, fig. 1, 3) figured a specimen of this species under the name *clathrata*, now known as a synonym of *P. atropurpurea* (Houart et al., 2019: 209).

**Etymology:** Named in the genitive case for the surname Murphy, a name representing Brendan and William Murphy, two individuals completely unknowingly of one another, but coincidentally with same last name. Brendan, a dear friend and high school colleague of the senior author, facilitated the first visit to the type locality of this species, a site where several specimens had subsequently been collected and examined for this description. William Murphy, a dear friend of the senior author's father, was gracious enough, along with wife Donna, to host Mr. Wiedrick at their residence in Humboldt County, an opportunity that afforded Mr. Wiedrick to conduct research in northern California field sites. Specimens sampled and identified as *P. grandilurida* from Shelter Cove, the city in which Mr. and Mrs. William Murphy resides, is also the type locality of that new species, the only location where this species was acquired and analyzed for spiral morphology.

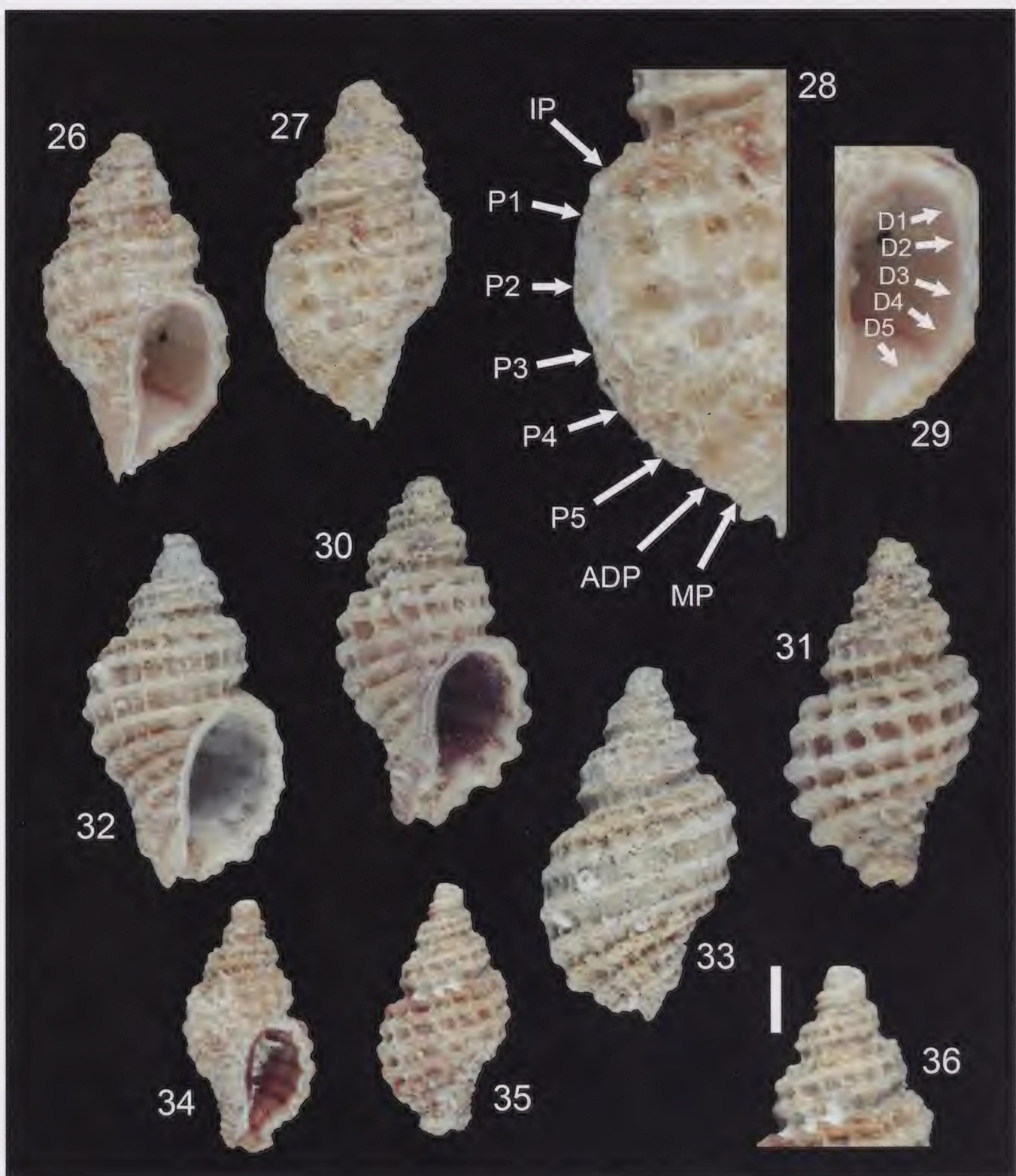
***Paciocenebrina pseudopusilla* new species**

(Figures 26-36)

CHRONOMY

*Ocenebra interfossa*.—Radwin and D'Attilio, 1976: pl. 20, fig. 11.

**Description:** Shell very small for genus, holotype worn, length 7.5 mm, width 5.8 mm, paratype juvenile, length 5.4 mm, width 3.0 mm. Shell ovate rhomboid, siphonal canal short, sculpture clathrate, axial ribs somewhat narrow, cord thickness moderate, interspaces squarish, large, color white to tan, pits slightly browner, occasionally



**Figure 26–36.** *Paciocenebrina pseudopusilla* new species. **26–27.** Holotype, China Rock, California, length 7.5 mm, width 5.8 mm (LACM 3764). **28.** Spiral cords morphology. **29.** Apertural denticles morphology. **30–31.** *P. pseudopusilla*, Neah Bay, Washington, length 7.5 mm, width 4.3 mm (SGW 121). **32–33.** Punta Popotla, Baja California, Mexico, length 7.6 mm, width 4.3 mm (SGW 122). **34–35.** Paratype, Jade Cove, California, on rock at 14.6 m, length 5.4 mm, width 3.0 mm, (LACM 3766). **36.** Protoconch, scale bar: 1.0 mm.

with sienna brown blotches on IP cord and/or P1 cord white, rarely one brown thin band on base, interior of aperture almost exclusively with dark brown band at cords. Spire moderately blunt, apex relatively blunt, tabulate, protoconch large, broad, whorl carination strong, shoulder and median cord almost equal in strength, large, distinct, slowly and subtly transitioning to clathrate sculpture, cords more spaced than in *P. pusilla*, scabrocity less evident than that species. First teleoconch whorl with P1, P2 spiral cords, second with P1, P2 cords, starting IP cord, third whorl with IP, P1, P2 cords, fourth with IP, P1, P2, P3, P4, P5, ADP, MP spiral cords, final whorl with 15 narrow, moderately spaced axial ribs. Aperture elongate ovate, moderately small, parietal and columellar wall extremely thin, canal rarely fused. Apertural denticle morphology somewhat weak, consisting of D1-D5.

**Type Material:** Holotype LACM 3764, length 7.5 mm, width 5.8 mm; paratype LACM 3766, length 5.4 mm, width 3.0 mm (Jade Cove, Monterey County, California (35°54'46" N, 121°28'29" W), on rocks at 14.6 m.

**Type Locality:** China Rock, Seventeen Mile Drive, Monterey County, California, (36°36'10" N, 121°57'42" W) on intertidal rocks.

**Other Material Examined:** Three specimens, in beach drift, Makah Bay, Clallam County, Washington, collected by Tom Rice [LACM 182327]; one specimen, Anchor Bay, Mendocino County, California, collected by D. Brown, July 1958 [LACM 61635]; one specimen, intertidal, Waddell Beach, Santa Cruz County, California (37°06'00" N, 122°19'59" W), collected by Hulda McLean, 1967-1968 [LACM 1967-95.60]; eight specimens at 18 m, Isle of St. James, North Farallon Islands, California (37°45'40" N, 123°05'57" W), collected by R.W. Schmieder, R/V CORDELL EXPLORER, 14 September 1991 [LACM 1991-177.23]; 23 specimens, intertidal on rocks, Carmel Point, Monterey County, California (36°31'00" N, 121°57'0" W), collected by J.H. McLean, 13-15 October 1981 [LACM 1981-47.25]; three specimens at 12.1-38.1 m, Carmel Submarine Canyon, north end San Jose Creek Beach, Monterey County, California (36°31'59" N, 121°55'59" W), collected by J.H. McLean, 1960-1964 [LACM 1960-24.106]; two specimens, intertidal on shale ledges and boulder reef, 0.4 km northwest of South Point, Shell Beach, San Luis Obispo County, California (35°09'18" N, 120°40'29" W), collected by P. I. LaFollette, 10 December 1977 [LACM 77-111.45]; one specimen, intertidal to 7.6 m, 0.48 km southeast of Bay Point, San Miguel Island, California Channel Ids., California (34°01'59" N, 120°17'59" W), collected by J.H. McLean, 21-22 August 1967 [LACM 1967-38.57]; one specimen, intertidal, Forney Cove, Santa Cruz Island, California Channel Ids., California (34°03'29" N, 119°55'00" W), collected by J.H. McLean, 15 March 1969 [LACM 1969-11.37]; two specimens at 23-27 m, on granite pinnacles, Wilson Rock, San Miguel Island, California Channel Ids., California (34°06'24" N, 120°23'41" W), collected by J.H. McLean, 31 May 1982 [LACM

1982-59.33]; 20 specimens at 9.1-30.4 m, Isthmus Cove, Santa Catalina Island, California Channel Ids., California (33°26'30" N, 118°28'59" W), collected by J.H. McLean, June-July 1971 [LACM 71-99.33]; six specimens at 9.1-21.3 m, Santa Barbara Island, California Channel Ids., California (33°28'59" N, 119°1'30" W), collected by J.H. McLean and J. Margetts, 8 July 1972 [LACM 72-97.38]; 13 specimens, San Pedro, Los Angeles County, California, collected by R.H. Tremper [LACM 59613]; five specimens, Laguna Beach, Orange County, California [LACM 17420]; two specimens from Reef Point, Orange County, California [LACM 17431]; three specimens, intertidal, south side of Punta Banda, Baja California, Mexico (31°43'36" N, 116°43'00" W), collected by J.H. McLean, 30 November 1963 [LACM 63-55.31]; 20 specimens at 15.2-30.4 m, Ben Rock, near Isla San Martin, Baja California, Mexico (30°25'59" N, 116°07'00" W), collected by J.H. McLean, 23 September 1972 [LACM 72-112.37]; five specimens at 13.7 m, northwest end of Isla Cedros, Baja California, Mexico (28°21'00" N, 115°14'48" W), collected by J.H. McLean, 24 September 1972 [LACM 72-114.36]; one specimen, intertidal, Punta Rompiente, Baja California, Mexico (27°43'22" N, 115°00'06" W), collected by J.H. McLean and P. I. LaFollette, R/V SEARCHER, 21 October 1971 [LACM 71-162.43].

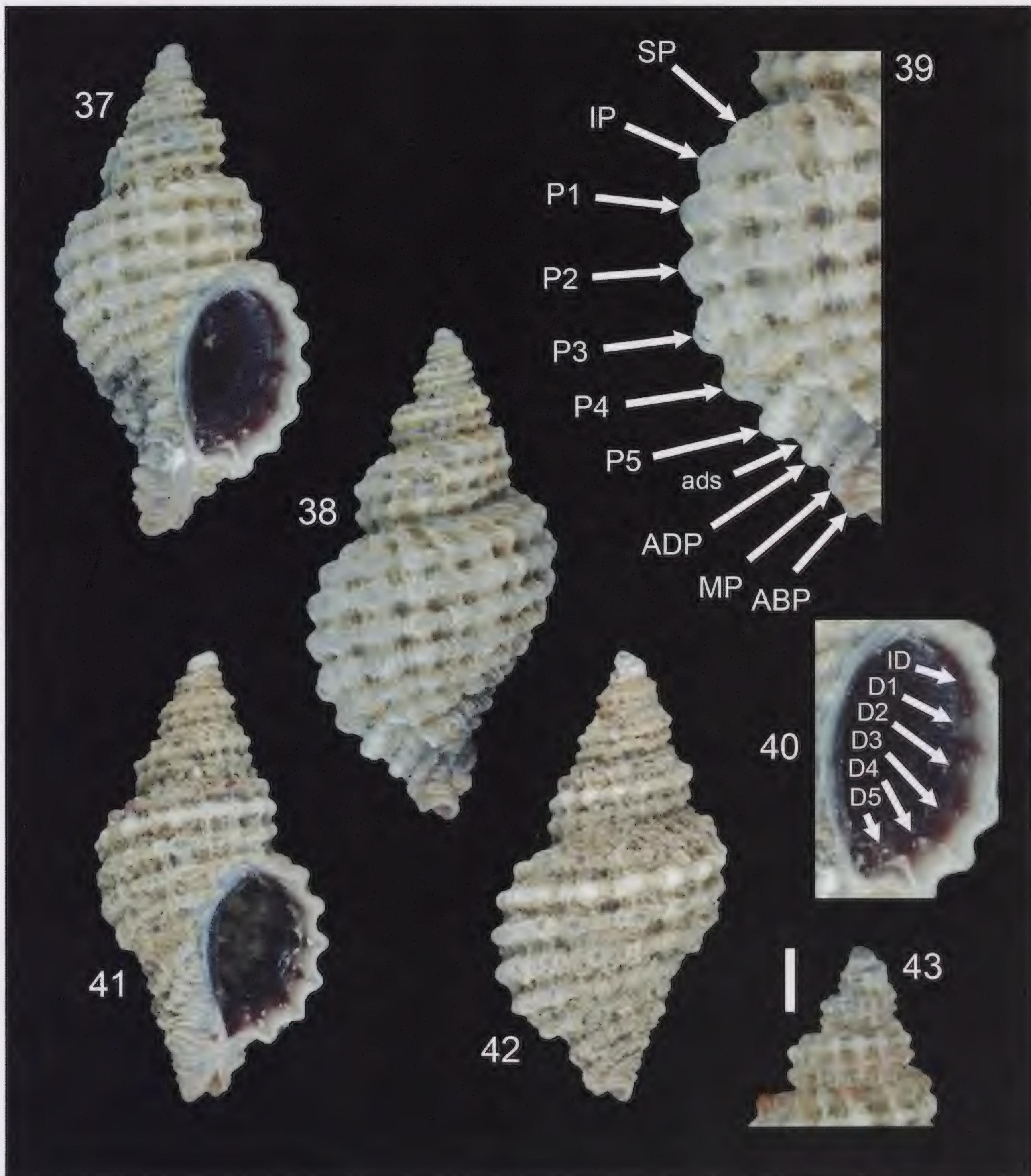
**Distribution:** Makah Bay, Clallam Co., Washington (48° N) to Punta Rompiente, Baja California Sur, Mexico (27° N); intertidal and subtidal zone on rocks to 125 m.

**Remarks:** The initial three teleoconch whorls are similar to *Paciocenebrina gracillima* (Stearns, 1871) (Figures 48-51), but *P. pseudopusilla* is absent of secondary cords. The general morphology is most similar to *P. pusilla*, protoconch features, spiral and denticle morphology (Figures 28-29, 39-40) are distinguishable characters in separating these species, considering additional characteristics is problematic and usually lend to improper identification. Protoconch of *P. pusilla* small, bulbous, highly erect, keel indistinct, *P. pseudopusilla* protoconch large, profile wide, tabulate, keel distinct, D6 cord present in *P. pusilla*, exclusively absent in *P. pseudopusilla*. Superficially similar to *P. pusilla*, initial two whorls identical, third whorl with P3 cord present in *P. pusilla*, absent in *P. pseudopusilla*, fourth whorl of *P. pusilla* with P6, s6 and ABP cords, D6 apertural denticle, and one fewer axial rib, characters not seen in *P. pseudopusilla*.

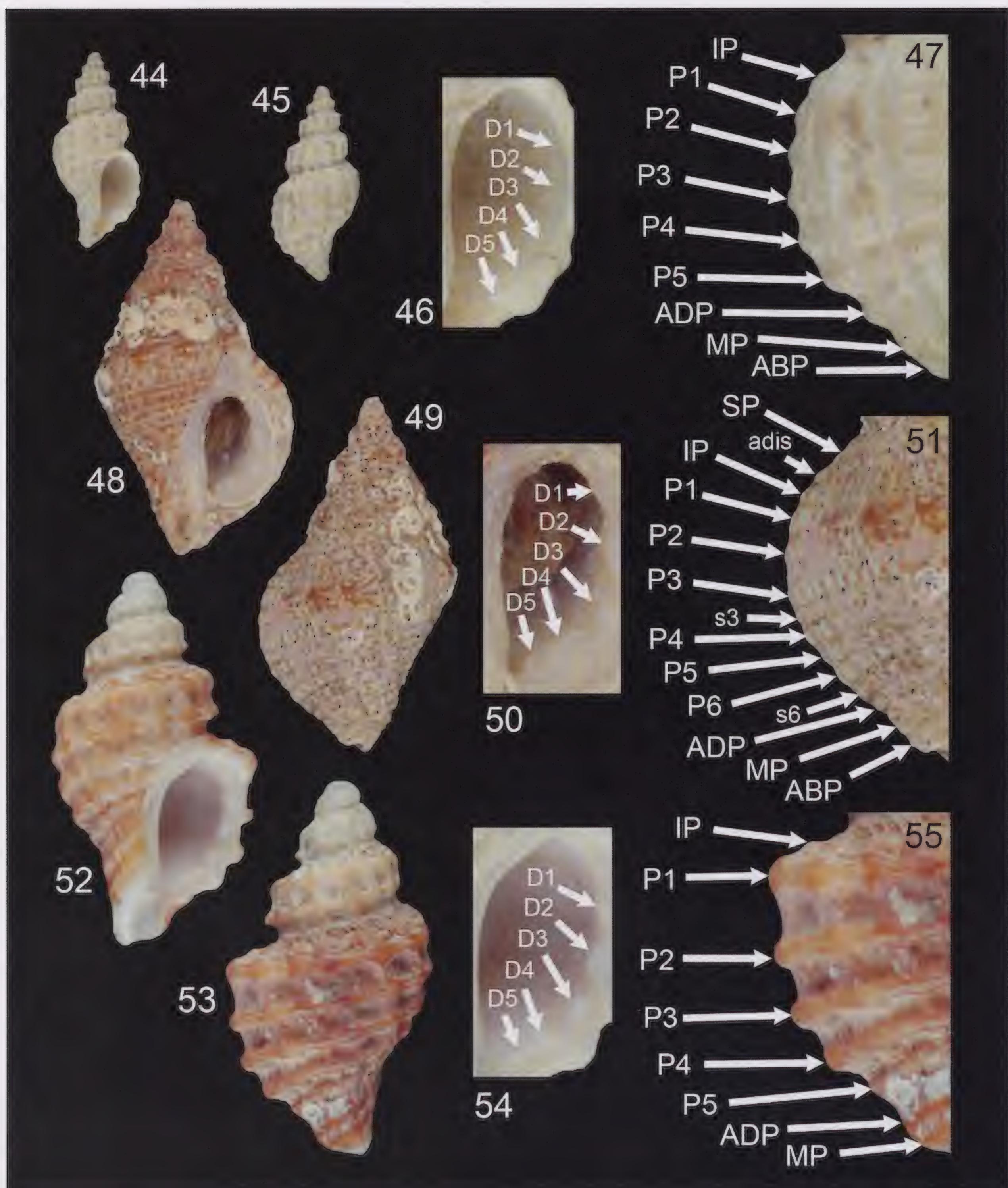
**Etymology:** Gender feminine, *pseudo-* meaning spurious and *pusilla* in reference to that morphologically similar species in the nominative case.

#### *Paciocenebrina pusilla* new species (Figures 37-43)

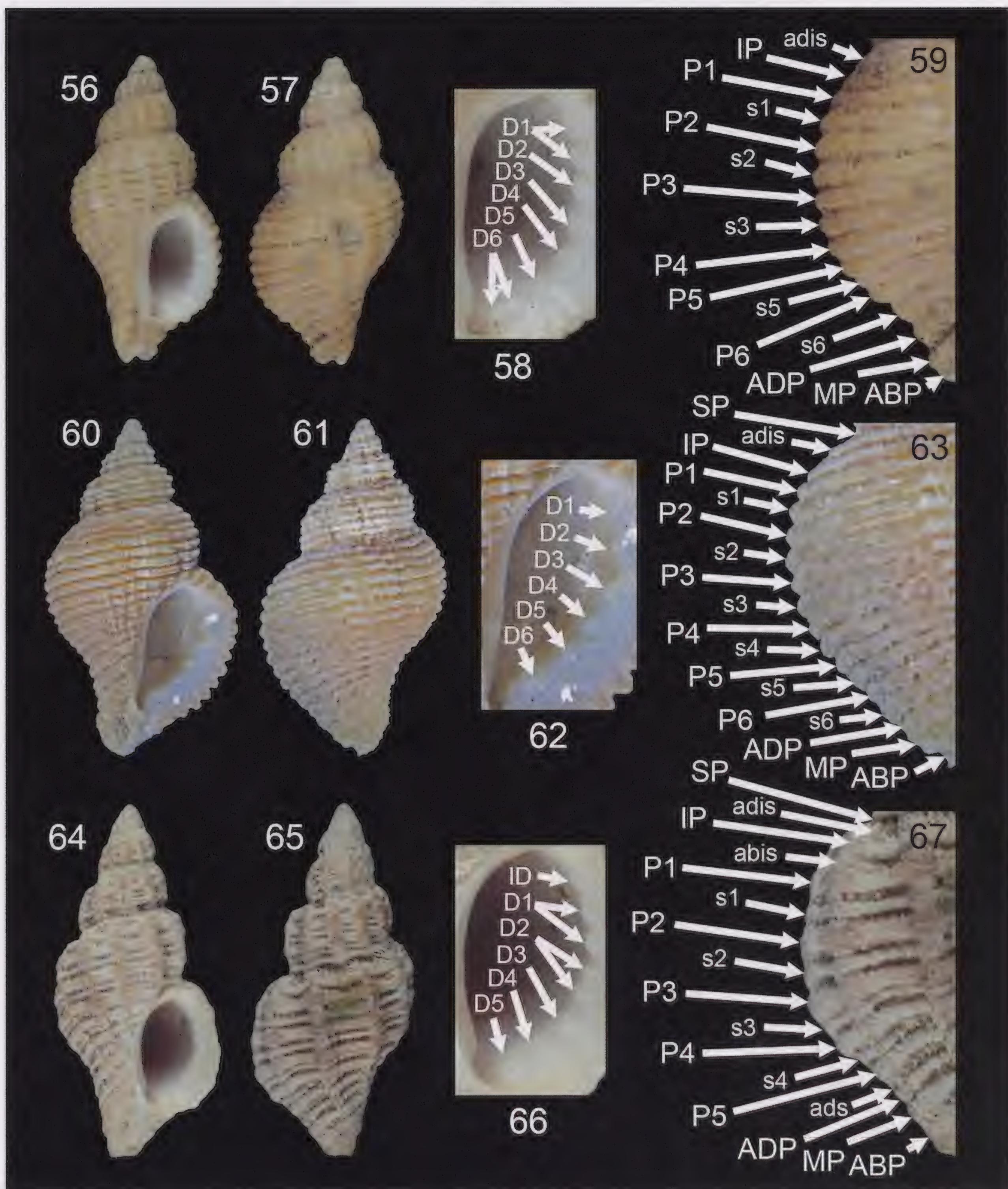
**Description:** Shell small for genus, holotype length 9.6 mm, width 5.2 mm. Shell elongate, rhomboid, sculpture clathrate, ribs somewhat tight, spiral cords thick, interspaces small, condensed, color white to dingy, gray brown, rarely with sienna brown blotches on IP cord, P1 cord often white, occasionally P3 cord with faint brown marks, interior of aperture dark purplish brown or white.



**Figures 37–43.** *Paciocenebrina pusilla* new species. **37–38.** Holotype, Point Estero, California, on intertidal rocks, length 9.6 mm, width 5.2 mm (LACM 3765). **39.** Spiral cords morphology. **40.** Apertural denticles morphology. **41–42.** Paratype, Cayucos, California, on intertidal rocks, length 8.8 mm, width 4.9 mm (LACM 3767). **43.** Protoconch, scale bar: 1.0 mm (SGW 123).



**Figures 44-55.** *Paciocenebrina* species. **44-47.** *Paciocenebrina minor* (Dall, 1919). **44-45.** Holotype, Santa Catalina Island, California, length 7.3 mm, width 3.7 mm (USNM 56912). **46.** Apertural denticles morphology. **47.** Spiral cords morphology. **48-51.** *Paciocenebrina gracillima* (Stearns, 1871). **48-49.** Syntype, at 18.2 m, San Diego, California, length 13.4 mm, width 7.4 mm (USNM 46920). **50.** Apertural denticles morphology. **51.** Spiral cords morphology. **52-55.** *Paciocenebrina atropurpurea* (Carpenter, 1865). **52-53.** Lectotype, Neah Bay, Washington, length 14.0 mm, width 7.6 mm (USNM 15528b). **54.** Apertural denticles morphology. **55.** Spiral cords morphology.



**Figures 56–67.** *Paciocinebrina* species. **56–59.** *Paciocinebrina munda* (Carpenter, 1864). **56–57.** Holotype, Santa Catalina Island, California, length 16.4 mm, width 8.3 mm (USNM 46708). **58.** Apertural denticles morphology. **59.** Spiral cords morphology. **60–63.** *Paciocinebrina lurida* (Middendorff, 1848). **60–61.** Syntype, Sitka, Alaska, length 18.0 mm, width 10.5 mm (ZISP 62131). **62.** Apertural denticles morphology. **63.** Spiral cords morphology. **64–67.** *Paciocinebrina interfossa* (Carpenter, 1864). **64–65.** Holotype, Monterey, California, length 18.8 mm, width 9.3 mm (USNM 4636). **66.** Apertural denticles morphology. **67.** Spiral cords morphology.

Spire acute, protoconch small, relatively erect, initially projecting upward, bulbous, keel weak, shoulder and median cord almost equal in strength, intersected immediately by clathrate sculpture transitioning to pustulated intersections with evenly-spaced ribs, scabrocity highly prominent on subsutural ramp, between cords and on siphonal canal. First two teleoconch whorls with IP, P1, P2 spiral cords, third with IP, P1, P2 cords, starting SP cord, fourth whorl with IP, P1, P2, P3, P4, P5, P6, s6, ADP, MP, ABP cords, 16 narrow, but tightly spaced axial ribs on final whorl. Aperture elongate ovate, moderately large, somewhat restricted, parietal and columellar wall extremely thin, canal almost exclusively fused. Denticle morphology absent or very weak, only detectable in fully matured specimens, D1-D6 denticles thereafter.

**Type Material:** Holotype LACM 3765, length 9.6 mm, width 5.2 mm; one paratype LACM 3767 (Cayucos, San Luis Obispo County, California (35°26'50" N, 120°55'14" W), on intertidal rocks).

**Type Locality:** Point Estero, San Luis Obispo County, California (35°27'34" N, 120°58'15" N), on intertidal rocks.

**Other Material Examined:** One specimen, intertidal on rocks, Carmel Point, Monterey County, California (36°31'0" N, 121°57'0" W), collected by J.H. McLean, 13-15 October 1981 [LACM 81-47.26]; four specimens, Pacific Grove, Monterey County, California, collected by A. G. Smith, 1910 [LACM 182324]; two specimens, Monterey, Monterey County, California, Falkenthal collection [LACM 182323]; three specimens, Monterey, Monterey County, California [LACM 182325]; five specimens, Monterey, Monterey County, California, collected by Howard Hill [LACM 182326]; one specimen, siftings from *Phyllospadix* roots, Hopkins Marine Station, Pacific Grove, Monterey County, California (36°37'30" N, 121°54'00" W), collected by J.H. McLean, 1 December 1962 [LACM 62-16.20]; one specimen, intertidal, Dinosaur Cave, Shell Beach, San Luis Obispo County, California (35°09'01" N, 120°40'36" W), collected by P.M. Oringer, 19 December 1968 [LACM 68-48.24]; two specimens, intertidal, near El Cortez Hotel, north of Ensenada, Baja California, Mexico (31°52'30" N, 116°40'48" W), collected by J.H. McLean and P.M. Oringer, 19 December 1964 [LACM 64-32.40]; one specimen, intertidal on rock ledges and boulders, 1.6 km south of Puerto Santo Tomás, Baja California, Mexico (31°34'59" N, 116°40'00" W), collected by J.H. McLean and P.M. Oringer, 4 January 1966 [LACM 66-1.47]; six specimens, intertidal, cement plant halfway between village and beach at Puerto Santo Tomás, Baja California, Mexico (31°33'00" N, 116°40'00" W), collected by J.H. McLean, 8-10 January 1967 [LACM 67-2.58].

**Distribution:** Carmel Point, Monterey Co. California (36° N) to south of Puerto Santo Tomás, Baja California, Mexico (31° N); chiefly intertidal on rocks. This species seems to inhabit cold waters to the north and reappears in the cold upwelling regions of northern Baja California.

**Remarks:** The first whorl with visible IP, P1 and P2 cords which is identical to other *Paciocenebrina* species, second whorl identical to *P. lurida* and *P. interfossa*, fourth and final whorl of *P. pusilla* lacking secondary cords not present in the other two species. See *P. pseudopusilla* section for comparisons of this similar species. This species is commonly confused as juvenile specimens of *Paciocenebrina atropurpurea* and *P. interfossa*.

**Etymology:** Gender feminine, *pusilla* meaning little in the nominative case.

## ACKNOWLEDGMENTS

We graciously thank Lindsey T. Groves (Collections Manager, Malacology Department, LACM) for access to the museum's collection, assistance with LACM voucher numbers, permission to analyze LACM material and essential literature at the LACM library, and for his suggestions that greatly improved the initial manuscript. Bernard Garrigues was additionally instrumental in providing constructive remarks which further refined the development of this work. We are also especially grateful to Elizabeth Kools (CASIZ), Erica Clites and Dave Strauss (UCMP), Andreia Salvador (NHMUK), Boris Sirenko (ZIN), and Ellen Strong (USNM) for either allowing access to respective collections or for sending images of specimens essential to the completion of this paper.

## LITERATURE CITED

Abbott, D.P. and E.C. Haderlie. 1980. Prosobranchia: marine snails. In: R.H. Morris, D.P. Abbott, and E.C. Haderlie (eds.), Intertidal invertebrates of California. Stanford University Press, Stanford, California, U.S.A., 230-307.

Abbott, R.T. 1968. Seashells of North America - A Guide to Field Identification. Golden Press, New York, New York, 280 pp.

Barco, A., G. Herbert, R. Houart, G. Fassio, and M. Oliverio. 2017. A molecular phylogenetic framework for the subfamily Ocenbrinae (Gastropoda, Muricidae). *Zoologica Scripta, Royal Swedish Academy of Sciences* 46(3): 322-335.

Bertsch, H. and L.E.A. Rosas. 2016. Marine Invertebrates of Northwest Mexico. Universidad Autónoma de Baja California, Ensenada, Baja California, México, 432 pp.

Bormann, M. 1946. Survey of some west American ocenebras, with the description of a new species. *The Nautilus* 60(2): 37-43.

Bouchet, P. 1990. Turrid genera and mode of development: the use and abuse of protoconch morphology. *Malacologia* 32(1): 69-77.

Bouchet, P. and E. Strong. 2010. Historical name-bearing types in marine molluscs: An impediment to biodiversity studies? In: A. Polaszek (ed.), *Systema Naturae*, CRC Press, London, England, United Kingdom: 63-74.

Brown, J.H. 2014. Why marine islands are farther apart in the tropics. *The American Naturalist* 183(6): 842-846.

D'Attilio, A. 1980. *Trophon painei* (Dall, 1903): an anomalous murex (Gastropoda, Muricidae, Trophoninae). *The Festivus* 12(1): 6-9.

D'Attilio, A. 1981. A preliminary report on some features of muricacean morphology. *The Festivus* 13(11): 118-125.

Davis, K.E., J. Hill, T.I. Astrop, and W.A. Wills. 2016. Global cooling as a driver of diversification in a major marine clade. *Nature Communications* 7(13003): 1–8.

Fair, R. H. 1976. The Murex book: an illustrated catalogue of Recent Muricidae (Muricinae, Muricopsinae, Ocenebrinae). Sturgis Printing Co., Honolulu, Hawaii, U.S.A., 138 pp, pls. 1–23.

Griffith, L.M. 1967. The intertidal univalves of British Columbia. Provincial Museum, Dept. of Recreation and Conversation, handbook 26, Victoria, British Columbia, Canada, 101 pp.

Hansen, T.A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6(2): 193–207.

Houart, R., G.J. Vermeij, and S.G. Wiedrick. 2019. Description of new taxa, lectotypes and neotype designations and new synonymy in Muricidae (Pagodulinae, Trophoninae, Ocenebrinae) from the Northeastern Pacific. *Zoosymposia* (James H. McLean Memorial Volume) 13: 184–241, figs. 1–25.

Jablonski, D. 1986. Larval ecology and macroevolution in marine invertebrates. *Bulletin of Marine Science* 39(2): 565–587.

Jablonski, D. and R. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Review* 58: 21–89.

Liff-Grieff, P. 2006. Ocinebrinas: California's "lesser" muricids. *Las Conchas* 38(2): 2–5, 7.

Marshall, D.J., P.J. Krug, E.K. Kupriyanova, M. Byrne, and R.B. Emlet. 2012. The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution and Systematics* 43: 97–114.

Mayhew, P.J., M.A. Bell, T.G. Benton, and A.J. McGowan. 2012. Biodiversity tracks temperature over time. *Proceedings of the National Academy of Sciences of the United States of America* 109(38): 15141–15145.

McConaughey, B.H. and E. McConaughey. 1985. The Audubon Society nature guides, the Pacific coast, a comprehensive field guide, fully illustrated with color photographs, to the birds, plants, seashore creatures, fishes, whales, and other natural wonders of North America's western shore, from Alaska to southern California. Alfred A. Knopf, New York, New York, U.S.A., 633 pp.

McLean, J.H. 1996. The Prosobranchia, The Mollusca pt. 2, The Gastropoda. In: P.H. Scott, J.A. Blake, and A. Lissner (eds.). *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Santa Barbara Museum of Natural History 9(2): 1–160.

McLean, J.H. 2007. Shelled Gastropoda. In: J.T. Carlton, (ed.), *The Light and Smith manual. Intertidal invertebrates from central California to Oregon*, 4<sup>th</sup> edition. University of California Press, Berkeley, pp. 713–753.

Merle, D. 1999. La radiation des Muricidae (Gastropoda: Neogastropoda) au Paléogène: approche phylogénétique et évolutive. Paris. Thèse de doctorat du Muséum national d'Histoire naturelle: i–vi, 1–499.

Merle, D. 2001. The spiral cords and the internal denticles of the outer lip in the Muricidae: terminology and methodological comments. *Novapex* 2(3): 69–91.

Merle, D. 2005. The spiral cords of the Muricidae (Gastropoda, Neogastropoda): importance of ontogenetic and topological correspondences for delineating structural homologies. *Lethaia* 38: 367–379.

Merle, D., B. Garrigues, and J.-P. Pointer. 2011. Fossil and recent Muricidae of the world, part Muricinae. Conchbooks, Hackenheim, Germany, 648 pp.

Merle, D. and R. Houart. 2003. Ontogenetic changes of the spiral cords as key innovation of the muricid sculptural patterns: the example of the *Muricopsis*-*Murexsul* lineages (Gastropoda: Muricidae: Muricopsinae). *Comptes Rendus de l'Académie des Sciences Palevol* 2: 547–561.

Middendorff, A.T. 1848. Vorläufige anzeige einiger neuer konchylien aus den geschlechtern: *Littorina*, *Tritonium*, *Bullia*, *Natica* und *Margarita*. *Bulletin de La Classe Physico-Mathématique de l'Académie Impériale des Sciences de Saint-Pétersbourg* 7(16): 241–246.

MolluscaBase eds. 2020. MolluscaBase. Ocenebrinae Cossmann, 1903. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=225324> on 2020-04-29

Myers, B.W. and A. D'Attilio. 1986. Comments on the protoconch in the Muricidae with illustrations. *The Festivus* 18(5): 55–77.

Nützel, A. 2014. Larval ecology and morphology in fossil gastropods. *Palaeontology* 57(3): 479–503.

Palmer, A.R. 1988. Feeding biology of *Ocenebra lurida* (Prosobranchia: Muricacea): diet, predator-prey size relations, and attack behavior. *The Veliger* 31(3/4): 192–203.

Ponder, W.F. and D.R. Lindberg. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119: 83–265.

Powell, A.W.B. 1966. The molluscan families Speightiidae and Turridae, an evaluation of the valid taxa, both recent and fossil, with lists of characteristic species. *Bulletin of the Auckland Institute and Museum* 5: 1–184.

Radwin, G.E. and A. D'Attilio. 1971. Muricacean supraspecific taxonomy based on the shell and the radula. *The Echo, Annual Report of the Western Society of Malacologists* 4: 55–67.

Radwin, G.E. and A. D'Attilio, 1976. *Murex Shells of the World. An illustrated Guide to the Muricidae*. Stanford University Press, Stanford, California, U.S.A., 284 pp., 32 pls., 192 text figs.

Rice, T. 1971. Marine shells of the Pacific Northwest. Ellison Industries, Inc., Edmonds, Washington, U.S.A., 102 pp.

Shuto, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* 7: 239–256.

Smith, A.G. and M. Gordon, Jr. 1948. The marine mollusks and brachiopods of Monterey Bay, California, and vicinity. *Proceedings of the California Academy of Sciences*, 4<sup>th</sup> series 26(8): 147–245.

Spight, T.M., C. Birkeland, and A. Lyons. 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). *Marine Biology* 24: 229–242.

Talmadge, R.R. 1975. A note on *Ocenebra lurida* (Middendorff). *The Veliger* 17(4): 414.

Vermeij, G.J. 1993. *A natural history of shells*. University Press, Princeton, New Jersey, U.S.A., 207 pp.

Wiedrick, S.G. 2018. A systematic revision of *Paciocinebrina* Houart, Vermeij & Wiedrick, MS (Gastropoda: Muricidae: Ocenebrinae) in Western North America. Unpub. MS thesis, California, State University, Fullerton, [ProQuest LLC., Ann Arbor, Michigan, U.S.A.], 256 pp.

# A new species of *Arca* (Bivalvia: Arcidae) from the lower Miocene Asahi Formation on the Japan Sea side of central Honshu, with remarks on the westward faunal migration from the eastern Pacific

**Kazutaka Amano**

Department of Geoscience  
Joetsu University of Education  
1 Yamayashiki  
Joetsu 943-8512, JAPAN

**Hirosi Kurita**

Department of Geology  
Faculty of Science  
Niigata University  
Niigata 950-2181, JAPAN

## ABSTRACT

The arcid bivalve, *Arca (Arca) budoensis* new species, is described from the Budo Mudstone Member of the Asahi Formation in northern Niigata Prefecture, central Honshu. The age of the member has been assigned to 16.6–15.9 Ma (late early Miocene) on the basis of dinoflagellate cysts. Judging from the arcid, dinoflagellate cysts and sedimentary facies, the paleoenvironment of the member was a shallow embayment influenced by a warm-water current. The reason that the molluscan fauna of the Budo Member contains no characteristic species of the subtropical to tropical Arcid-Potamid fauna (17.0–16.7 Ma) is that the Budo fauna is slightly later than that Arcid-Potamid fauna. Because the new species resembles fossil and Recent species of the eastern Pacific, *A. budoensis* is accepted as derived from an ancestor that migrated westward to Asia. **The senior author, Kazutaka Amano, is the single author of the new species.**

*Additional Keywords:* Marine, fossil, shallow sea, warm-current

## INTRODUCTION

The Japan Sea was formed in the latest Oligocene (ca. 25 Ma) by separation of the Japanese Islands from the Eurasian continent (Yanai et al., 2010). The oldest “marine” trace fossils from the Japan Sea side were recovered from the Shiose-no-Misaki sediments which were intruded by a dolerite dated at 20 Ma (Ohguchi et al., 2005). However, Sato et al. (2009) argued that these fossils were non-marine. According to Sato et al. (1991, 2009), the oldest marine fossils including the nannofossil, *Sphenolithus heteromorphus* were from the lower part of the NN4 zone (Martini, 1971), later than 17.75 Ma according to Backman et al. (2012).

In the northern part of Niigata Prefecture, the marine sediments occur in the Miocene Asahi Formation (Nishida, 1958; Takahama et al., 1976), which unconformably overlies the Tenjosan Formation and is overlain by the Osudo Shale containing the Osudo flora (Kamoi et al., 1978). This flora corresponds with the late early to early Middle Miocene Daijima-type flora (Takahama

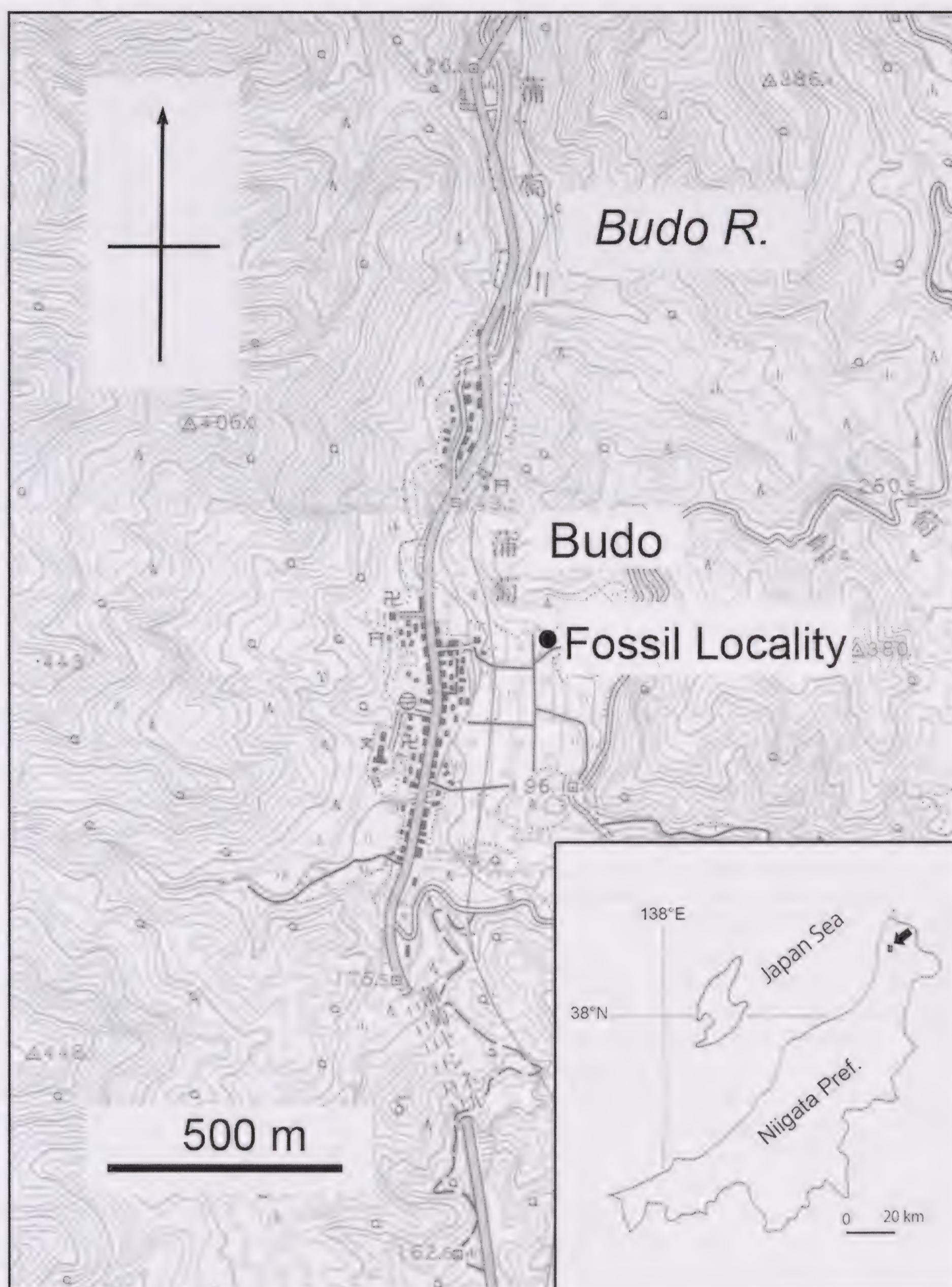
et al., 1976; Kamoi et al., 1978). The Asahi Formation consists of the Budo Mudstone, Nagasakatoge Rhyolite and Arasawa Sandstone and Conglomerate Members in ascending order (Takahama et al., 1976). The large foraminifer *Operculina complanata japonica* Hanzawa, from the Arasawa Member indicates a late early to early late Miocene age (Kamoi et al., 1978).

The following mollusks and brachiopods (including *Terebratulina* spp.) were recorded from the Budo Member by Nishida (1958), Tsuda (1965) and Takahama et al. (1976): *Chlamys iwasakiensis*, *Pecten* sp., *Cardium* sp., *Geloina yamanei*, *Panomya simotomensis*, and *Littolinopsis miodelicatula*. Of these, *Geloina yamanei* and *Littolinopsis miodelicatula* are characteristic species of late early Miocene mangrove swamp fauna (Oyama, 1950). However, these species names were only listed up from unknown localities and have never been described nor illustrated. Moreover, the exact age of this member has not been determined from microfossils.

Many marine fossils have been recovered from a previously unknown locality in the Budo Member. The species composition including a new arcid species is very different from the above listed species. In this paper, we determine the age by dinoflagellate cysts, describe the new bivalve species of *Arca* and discuss the paleobiological significance of the fauna.

## MATERIALS AND METHODS

The fossils were collected from a small outcrop along a rice field at 250m east from Budo (Figure 1; 38°23'23" N, 139°33'27" E). At the fossil locality, hard gray mudstones yielding many shell-dissolved fossils are exposed. From this locality, the following molluscan species are recorded: ***Arca budoensis* new species**, *Arcuatula*? sp. and *Cavilucina*? sp. Moreover, the fossils also include three species of brachiopods: *Discinisca* sp., *Coptothyris grayi* (Davidson), *Terebratalia* sp. and one fragment of Cirripedia, *Capitulum*? sp.



**Figure 1.** Locality of fossils. Base map from “Budo”, original scale 1:25,000; topographical map published by the Geospatial Information Authority of Japan.

Dinoflagellate cysts were picked for age determination from the rock subsampled in the mollusk-bearing mudstone. Taxonomic identification of dinoflagellate cysts follows Fensome et al. (2008), where complete bibliographic references were provided. The sample was treated successively with HCl and HF to eliminate carbonate and silicate minerals. Then heavy liquid zinc bromide (specific gravity 2.0) was used to concentrate organic particles from the residues after the acid treatment.

We used digital calipers (Mitsutoyo Company, model CD-20) to measure specimens of *Arca* to the first decimal

place. The terminology on *Arca* is follows Noda (1966). All specimens of *Arca* are deposited at the National Museum of Nature and Science, Tsukuba (NMNS).

#### DINOFLAGELLATE AGE

The sample yielded a number of dinoflagellate cysts whose preservation was sufficiently good for identification. Based on 393 counted specimens, the dinoflagellate cyst assemblage is characterized by abundant to common

occurrences of *Achomosphaera ramulifera*, *A. spongiosa*, *Cribroperidinium giuseppei*, *C. granomembranaceum*, *Diphyes latiusculum*, *Heteraulacacysta campanula*, *Hystrichokolpoma rigaudiae*, *Lingulodinium machaerophorum*, *Operculodinium centrocarpum*, *Spiniferites pseudofurcatus* and *Systematophora placacantha* with fewer *Nematosphaeropsis lemniscata*, *Reticulatosphaera actinocoronata*, and *Tuberculodinium vancampoae*. In the assemblage, protoperidinioid species are very minor in abundance and include *Brigantedinium* sp., *Lejeunecysta* spp., and *Selenopemphix nephroides* (Table 1). In addition, a few specimens of an acritarch species *Paralecaniella indentata* and a freshwater green alga *Pediastrum* sp. were also recorded.

The abundant to common occurrences of *Cribroperidinium giuseppei*, *C. granomembranaceum*, *Diphyes latiusculum*, *Spiniferites pseudofurcatus* and *Systematophora placacantha* indicate evident correlation with the basal part of the Subzone b of *Diphyes latiusculum* Zone originally proposed by Matsuoka et al. (1987) and subsequently modified by Obuse and Kurita (1999). According to Obuse and Kurita (1999), this part is coeval

**Table 1.** List of dinoflagellate cysts and acritarchs associated with the molluscan fossils. Relative abundance of each dinoflagellate cyst taxon is expressed as VA (very abundant, 20 % and more of the total specimen count), A (abundant, 20–10 %), C (common, 10–3 %), R (rare, 3–1 %) and VR (very rare, less than 1 %).

Species	Abundance
<b>DINOFLAGELLATA</b>	
<i>Achomosphaera ramulifera</i>	C
<i>Achomosphaera spongiosa</i>	C
cf. <i>Achomosphaera spongiosa</i>	R
<i>Batiacasphaera</i> ? spp.	VR
<i>Brigantedinium</i> sp.	VR
<i>Cleistosphaeridium ancyrea</i>	VR
<i>Cribroperidinium giuseppei</i>	C
<i>Cribroperidinium granomembranaceum</i>	C
<i>Diphyes latiusculum</i>	C
<i>Heteraulacacysta campanula</i>	R
<i>Hystrichokolpoma rigaudiae</i>	R
<i>Impagidinium</i> sp.	VR
<i>Lejeunecysta</i> spp.	VR
<i>Lingulodinium machaerophorum</i>	C
<i>Lingulodinium</i> sp.	VR
<i>Nematosphaeropsis lemniscata</i>	VR
<i>Operculodinium centrocarpum</i>	C
<i>Reticulatosphaera actinocoronata</i>	VR
<i>Selenopemphix nephroides</i>	VR
<i>Spiniferites membranaceus</i>	R
<i>Spiniferites pseudofurcatus</i>	C
<i>Spiniferites ramosus</i>	R
<i>Spiniferites</i> sp.	A
<i>Systematophora placacantha</i>	VA
<i>Tuberculodinium vancampoae</i>	R
<b>Other organic algal microfossils</b>	
<i>Paralecaniella indentata</i>	present
<i>Pediastrum</i> sp.	present

with the diatom *Denticulopsis praelauta* Zone (NPD3B) that is calibrated to the age interval of 16.6–15.9 Ma (latest early Miocene) by Yanagisawa and Akiba (1998) and Watanabe and Yanagisawa (2005).

## SYSTEMATICS

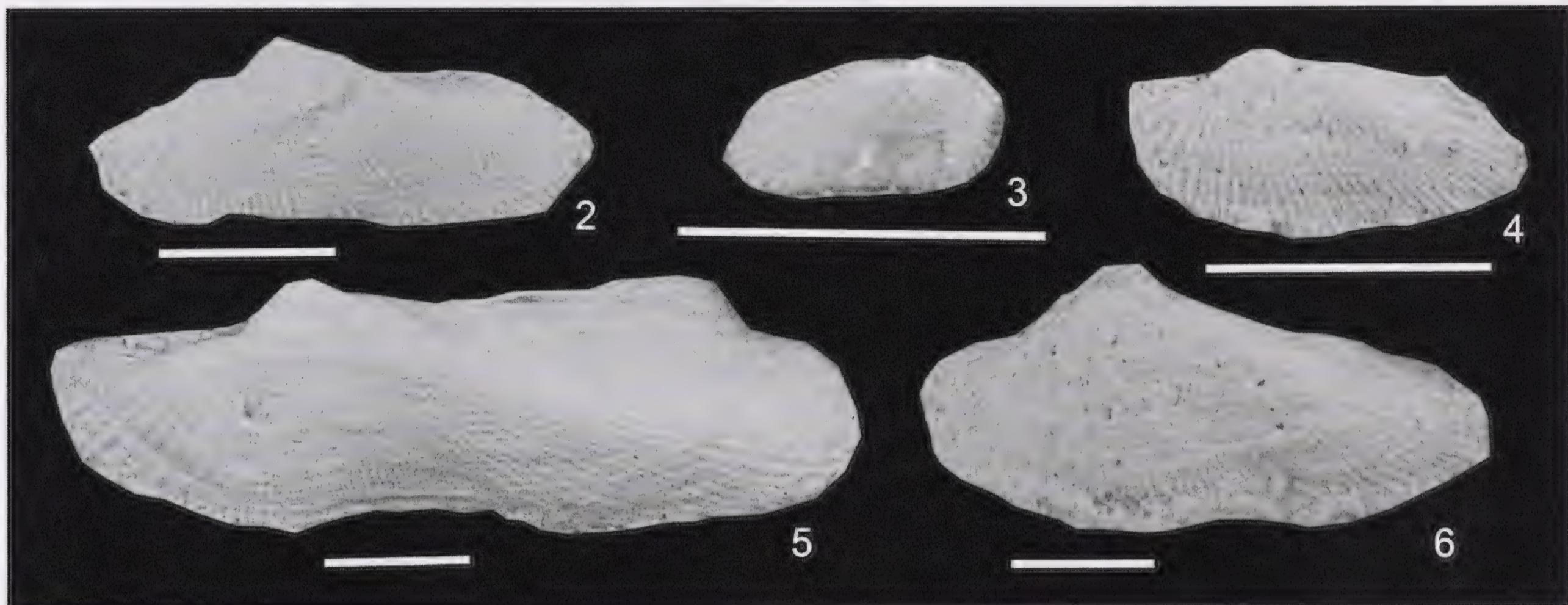
Family *Arcidae* Lamarck, 1809  
Subfamily *Arcinae* Lamarck, 1809  
Genus *Arca* Linnaeus, 1758  
Subgenus *Arca* Linnaeus, 1758

**Type Species:** *Arca noae* Linnaeus, 1758 by subsequent designation.

**Remarks:** The senior author, Kazutaka Amano, is the single author of the new species. Reinhart (1935) recognized four subgenera: *Arca*, *Litharca* Gray, 1842, *Arcoptera* Heilprin, 1887, and *Eonavicula* Arkell, 1929. According to Lutaenko and Maestrati (2007), *Litharca* is an independent genus and *Arcoptera* is independent from *Arca* (s.s.). Oliver and Chesney (1994) recognized *Tetrarca* Nordsieck, 1969 (type species: *Arca tetragona* Poli, 1795). When Oliver and Holmes (2006) subdivided *Arca* into *A. noae*, *A. avellana*, and *A. tetragona* groups, they did not treat the last group as a separate subgenus. Consequently, Lutaenko and Maestrati (2007) separated the extinct *Arcoptera* as a subgenus and *Arca* (s. s.) into three types: Type 1 (*A. avellana*, *A. boucardi*, *A. tetragona*), Type 2 (*A. navicularis*, *A. pacifica*, *A. zebra*) and Type 3 (*A. koumaci*), based on the presence of postero-dorsal wing and posterior sulcus. Huber (2010) subdivided the modern *Arca* into four subgenera as *Arca* (s. s.), *Tetrarca*, unnamed I (*A. avellana*, *A. imbricata*, *A. mutabilis*, *A. ventricosa*) and unnamed II (*A. boucardi*). From the view point of valve margins, Vermeij (2013) subdivided *Arca* into three groups as *A. imbricata* group with smooth edge (*A. avellana*, *A. imbricata*, *A. mutabilis*), *A. zebra* group with obsolete ventral crenulations and well-developed anterior and posterior ones (*A. zebra*, *A. pacifica*, *A. navicularis*, *A. ventricosa*, *A. noae*). Vermeij (2013) separated *A. boucardi* from these two groups by its continuously crenulated ventral margin and a much narrower hinge plate. Molecular data by Feng et al. (2015) and Kong et al. (2020) support the subdivision of *Arca* (s. s.) by Oliver and Holmes (2006) and Lutaenko and Maestrati (2007) except for the separation of *A. boucardi* as a subgenus level supporting Huber's (2010) and Vermeij's (2013) opinions. In this paper, the new species is treated as a *A. noae* group (Subgenus *Arca* s. s.) from its shell shape.

### *Arca (Arca) budoensis* Amano new species (Figures 2–6)

**Diagnosis:** Small *Arca* having low elongate shell, pointed anterior end, truncated posterior margin, strong radial ridge from umbo to postero-ventral corner and posterior sulcus. Surface ornamented with 64 radial ribs and granulated with growth lines on posterior part.



**Figures 2—6.** *Arca (Arca) budoensis* Amano new species. 2. Paratype, left valve, NMNS PM 65048. 3. Paratype, right valve, NMNS PM 65050. 4. Paratype, left valve, NMNS PM 65049. 5. Holotype, left valve, NMNS PM 65046. 6. Paratype, left valve, NMNS PM 65047. Scale bars = 5 mm.

**Description:** Shell small (to 25.8 mm long), elongate quadrate, much lower than high especially in adults ( $H/L = 0.33$  to  $0.56$ ), inequilateral ( $AL/L = 0.27$  to  $0.41$ ), strong radial ridge extending from umbo to postero-ventral corner. Antero-dorsal margin straight and horizontal; anterior end of dorsal margin pointed; antero-ventral margin posteriorly oblique; middle to posterior ventral margin broadly concave as byssal notch in adult but straight in younger specimens (length  $<7.3$  mm); postero-ventral corner acutely rounded; posterior margin subtruncated and concave; postero-dorsal margin straight and horizontal making right angle with posterior margin. Umbo produced above dorsal margin; beak located at anterior about one-third to two-fifths. Surface of anterior part of shell in front of radial ridge ornamented with 51 flat and fine radial ribs separated by nearly equal inter-spaces; anterior eight stronger than other ribs; posterior area of shell behind radial ridge sculptured by 13 radial ribs, lamellated growth ribs making granules at their crossing points; granulation sometimes seen in front of radial ridge in younger shells. Small taxodont teeth observable in terminal of hinge. Inner structure unknown.

**Type Material:** Holotype: Left valve (NMNS PM no. 65046), length 25.8 mm, height 8.6 mm, anterior length 7.6 mm. Paratypes: Left valve (NMNS PM no. 65047), length 19.6 mm, height 7.7 mm, anterior length 8.0 mm; left valve (NMNS PM nos. 65048), length 13.8 mm, height, 5.0 mm+; left valve (NMNS PM no. 65049), length 7.3 mm, height 4.1 mm, anterior length 2.9 mm; right valve (NMNS PM no. 65050), length 3.7 mm, height 1.9 mm, anterior length 1.0 mm.

**Type Locality:** 250m east from Budo, Murakami City; upper lower Miocene Budo Mudstone Member of Asahi Formation.

**Material Examined:** Twenty-eight specimens from the type locality.

**Remarks:** From the point of view of shell shape, there is no similar modern or fossil species in Japan. *Arca* sp. from the uppermost lower Miocene Kubohara Formation in Gifu Prefecture by Itoigawa et al. (1981, 1982) has a similar shell size and an elongate shell. However, *Arca (Arca) budoensis* new species has a pointed anterior end and lower shell than *Arca* sp.

*Arca (Arca) budoensis* new species can be included in the *A. noae* group of Oliver and Holmes (2006) and Type 2 by Lutaenko and Maestrati (2007) because of its wing shape and posterior sulcus. In the western Pacific, there is no fossil record other than the modern species, *Arca (Arca) navicularis* Bruguière, 1789 belonging to the same group and type. However, the oldest record of *A. (A.) navicularis* is from the Pliocene in Indonesia (Kase et al., 2008). *Arca (Arca) budoensis* new species differs from *A. (A.) navicularis* by having a lower shell, no pointed postero-dorsal end and finer radial ribs. In contrast, some similar species have been described from the eastern Pacific. *Arca (Arca) cf. hawleyi* Reinhart, 1943 from the Eocene Tejon Formation in California, is similar to the new species by having a similar size elongated shell with a pointed anterior end and a strong ridge from beak to postero-ventral corner. However, *Arca (Arca) budoensis* new species has a more posteriorly situated beak and more distinct radial ribs. A Recent species, *Arca (Arca) pacifica* (Sowerby, 1833) from Baja California to the Galápagos Islands (Coan and Valentich-Scott, 2012) is similar to the new species in having pointed anterior end and a concave area behind the strong ridge from beak to postero-ventral margin. However, *Arca (Arca) budoensis* new species has a lower elongate-quadrate shell, no pointed posterior end, shallower byssal notch and more numerous fine radial ribs and is much smaller than *A. (Arca) pacifica*. Another similar species is *Arca (Arca) truncata* (Sowerby, 1833) from San Lucas, Baja California

to the Galápagos Islands (Coan and Valentich-Scott, 2012). It resembles *Arca (Arca) budoensis new species* in its low elongate quadrate outline. *Arca (Arca) budoensis new species* has a pointed antero-dorsal end, a posterior sulcus and an oblique posterior margin which are never observed in the much larger *A. (A.) truncata*.

**Distribution:** Only from the type locality.

**Etymology:** Named for locality from where this species was collected.

## DISCUSSION

The present paper is the first to describe and illustrate fossils from the Budo Member. *Arca (Arca) budoensis new species* and its associated species indicate a shallow-marine environment. The occurrences of the dinoflagellate cysts *Lingulodinium machaerophorum* (cold-intolerant/thermophilic) and *Tuberculodinium vancampae* (tropical to subtropical) suggest the influence of a warm current (Head, 1997; de Vernal and Marret, 2007). Moreover, the occurrence of a freshwater alga *Pediastrum* sp. suggests proximity to a river that fed the embayment. This inference was also supported by the sedimentary facies analysis (Igarashi and Kurita, 2007). The shallow-marine molluscan fauna herein described is different from the tropical to subtropical Arcid-Potamid fauna (Tsuda, 1965), despite them sharing a similar paleoenvironment. Recently Yanagisawa and Watanabe (2017) postulated that the occurrence of the Arcid-Potamid fauna in Japan was confined to the interval of 17.0 to 16.7 Ma. As the Budo Member was deposited slightly later (16.6 to 15.9 Ma) than the Arcid-Potamid fauna, it does not include any characteristic species of the fauna. However, most species of Type 2 and the *Arca noae* group to which *Arca (Arca) budoensis new species* belongs live in warm water which is concordant with the paleoenvironment inferred by the dinoflagellate cysts.

As described here, *Arca (Arca) budoensis new species* resembles both fossil and modern species from the eastern Pacific, not from the western Pacific. In the early Miocene, six bivalve genera and one subgenus have been recognized as immigrants from the eastern Pacific to the west during the early to early middle Miocene. The taxa include the venerids *Securella*, *Kaneharaia*, *Compsomyax*, the hiattelid *Panomya*, the rock-boring myid *Platyodon*, the Pholadid *Penitella*, and the tellinid subgenus *Rexithaerus* (Amano, 2005). One modern species of the Type 2 (Lutaenko and Maestrati, 2007) in the western Pacific, *Arca (Arca) navicularis* first appeared only in the Pliocene of Java, Indonesia (Kase et al., 2008). Thus, *Arca (Arca) budoensis new species* was derived from the ancestor which migrated from the eastern Pacific to Japan at least by the early Miocene.

## ACKNOWLEDGMENTS

We are grateful to Geerat J. Vermeij (UC Davis) for his critical reading of the manuscript and useful suggestions.

We thank Sven N. Nielsen (Universidad Austral de Chile) and an anonymous reviewer for their useful comments. We also thank Kazuo Kawauchi (Niigata University of Pharmacy and Applied Life Sciences) and Yukihiko Kamoi (Niigata City) for kindly helping one of the authors, KA to collect the molluscan species.

## LITERATURE CITED

Amano, K. 2005. 6. Migration and adaptation of late Cenozoic cold-water mollusks in the North Pacific. In: Elewa, M. T. ed., *Migration of Organisms*: 127–150. Springer-Verlag, Berlin, Heidelberg.

Arkell, W.J. 1929. A monograph of British Corallian Lamellibranchia. Palaeontographic Society of London 1: 1–72.

Backman, J., I. Raffi, D. Rio, E. Fornaciari, and H. Pälike. 2012. Biozonation and biochronology of Miocene through Pleistocene calcareous nannofossils from low and middle latitudes. *Newsletters on Stratigraphy* 45: 221–244.

Bruguière, J.G. 1789. *Encyclopédie méthodique. Histoire naturelles des vers*. Paris 1: 1–344.

Coan, E.V. and P.H. Valentich-Scott. 2012. Bivalve Seashells of Tropical West America marine Bivalve mollusks from Baja California to Northern Peru. Santa Barbara Museum of Natural History, Monographs 6, 1258 pp.

de Vernal, A. and F. Marret. 2007. Organic-walled dinoflagellate cysts: tracers of sea-surface conditions. In: Hillaire-Marcel, C. and A. de Vernal, ed. *Proxies in Late Cenozoic paleoceanography. Developments in Marine Geology* 1: 371–409.

Feng, Y., Q. Li and L. Kong. 2015. Molecular phylogeny of Arcoidea with emphasis on Arcidae species (Bivalvia: Pteriomorpha) along the coast of China: Challenges to current classification of arcoids. *Molecular Phylogenetics and Evolution* 85: 189–196.

Fensome, R.A., R.A. MacRae, and G.L. Williams. 2008. DINOFLAJ2, Version 1. American Association of Stratigraphic Palynologists, Data Series no. 1.

Gray, J.E. 1942. Molluscs. In: *Synopsis of the contents of the British Museum*, ed. 44: 48–92. Woodfall & Son, London.

Head, M.J. 1997. Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern England. *Journal of Paleontology* 71: 165–193.

Heilprin, A. 1887. Explorations on the west coast of Florida and in the Okeechobee wilderness: with special reference to the geology and zoology of the Floridian peninsula: a narrative of researches undertaken under the auspices of the Wagner Free Institute of Science of Philadelphia. *Transactions of the Wagner Free Institute of Science of Philadelphia* 1: 1–134.

Huber, M. 2010. *Compendium of Bivalves*. ConchBooks, Hackenheim, 901 pp.

Igarashi, Y. and H. Kurita. 2007. Development of the Miocene rifts in the Oami-Hongo area, Yamagata Prefecture, and Budo area, Niigata Prefecture, Uetsu Mountains, NE Japan. *Abstracts from the 114th Annual Meeting of the Geological Society of Japan*: 226. (in Japanese)

Itoigawa, J., H. Shibata, H. Nishimoto, and K. Okumura. 1981. Miocene fossils of the Mizunami Group, central Japan. 2. Molluscs. *Monograph of the Mizunami Fossil Museum* 3-A: 1–53, pls. 1–52. (in Japanese)

Itoigawa, J., H. Shibata, H. Nishimoto, and K. Okumura. 1982. Miocene fossils of the Mizunami Group, central Japan. 2. Molluscs (Continued). *Monograph of the Mizunami Fossil Museum* 3-B: 1–330. (in Japanese)

Kamoi, Y., I. Kobayashi, and K. Suzuki. 1978. The middle Miocene Osudo fossil flora in the northern part of Niigata Prefecture. *Journal of the Geological Society of Japan* 84: 15–21. (in Japanese with English abstract)

Kase, T., Y. Kurihara, H. Hayashi, H. Pandita, and Y.M. Aguilar. 2008. Age refinement of the Sonde Molluscan Fauna, East Java, Indonesia. *Memoirs of the National Museum of Nature and Science, Tokyo* 45: 127–138.

Kong, L., Y. Li, K.M. Kocote, Y. Yanga, L. Qia, Q. Li, and K.M. Halanych. 2020. Mitogenomics reveals phylogenetic relationships of Arcoida (Mollusca, Bivalvia) and multiple independent expansions and contractions in mitochondrial genome size. *Molecular Phylogenetics and Evolution* 150: <https://doi.org/10.1016/j.ympev.2020.106857>.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima. Laurentius Salvius, Holmiae*, 824 pp.

Lamarck, J.B.P.A. de. 1809. *Philosophie zoologique; ou, exposition des considérations relatives à l'histoire naturelle des animaux, la diversité de leur organisation et des facilités qu'ils en obtiennent, aux causes physiques qui main tiennent en eux la vie, et donnent lieu aux mouvements qu'ils exécutent; enfin, à celles qui autres l'intelligence de ceux qui en sont doués*. Vol. 1: 422 pp., Vol. 2: 473 pp.

Lutaenko, K.A. and P. Maestrati. 2007. A new species of *Arca* L., 1758 (Bivalvia: Arcidae) from New Caledonia, with comments on the genus. *Korean Journal of Malacology* 23: 155–164.

Martini, E. 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci, A. ed. *Proc. 2nd International Conference of Planktonic Microfossils Roma: Rome (Ed. Tecnosc.)* 2, pp. 739–785.

Matsuoka, K., J.P. Bujak, and T. Shimazaki. 1987. Late Cenozoic dinoflagellate cyst biostratigraphy from the west coast of northern Japan. *Micropaleontology* 33: 214–229.

Nishida, S. 1958. Some considerations concerning the Green Tuff Regions in Japan. *The Cenozoic Research (Shinseidai No Kenkyu)* 27: 8–21. (in Japanese)

Noda, H. 1966. The Cenozoic Arcidae of Japan. *Science reports of the Tohoku University, 2<sup>nd</sup> Series (Geology)* 38: 1–161.

Nordsieck F. 1969. *Die europäischen Meeressmuscheln. Vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer*. Gustav Fischer, Stuttgart, 256 pp.

Obuse, A. and H. Kurita. 1999. Neogene dinoflagellate cyst biostratigraphy in northern Japan. Abstracts from the 1999 Annual Meeting of the Palaeontological Society of Japan: 95. (in Japanese)

Ohguchi, T., T. Yamazaki, H. Noda, K. Sasaki, and K. Kano. 2005. Marine sediments older than 20 Ma in the Oga Peninsula, NE Japan. *Journal of the Japanese Association for Petroleum Technology* 70: 207–215. (in Japanese with English abstract)

Oliver P.G. and H.C.G. Chesney. 1994. Taxonomy of Arabian Bivalves. Part 1. Arcoidea. *Journal of Conchology* 35(1): 17–31.

Oliver P.G. and A. N., Holmes. 2006. The Arcoidea (Mollusca: Bivalvia): a review of the current phenetic-based systematics. *Zoological Journal of the Linnean Society* 148: 237–251.

Oyama, K. 1950. Studies of fossil molluscan biocoenosis, no. 1, Biocoenological studies on the mangrove swamps, with descriptions of new species from Yatsuo Group. *Report of the Geological Survey of Japan* 132: 1–15.

Poli, J.X. 1795. *Testacea utriusque siciliae eorumque historia et anatomie tabulis aeneis illustrata*. Parma, Regio Typographio 2, pp. 75–264.

Reinhart, P. W. 1935. Classification of the pelecypod family Arcidae. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 11: 1–68.

Reinhart, P. W. 1943. Mesozoic and Cenozoic Arcidae from the Pacific Slope of North America. *Geological Society of America, Special Papers* 47: 1–117.

Sato, T., K. Baba, T. Ohguchi, and T. Takayama. 1991. Discovery of early Miocene calcareous nannofossils from Japan Sea side, northern Honshu, Japan, with reference to paleoenvironment in the Daijima and Nishikurosawa Ages. *Journal of the Japanese Association for Petroleum Technology* 56: 263–279. (in Japanese with English abstract)

Sato, T., M. Yamazaki and S. Chiyonobu. 2009. Geology of Akita Prefecture. *Daichi* 50: 70–79. (in Japanese)

Sowerby, G. B., I. 1833. Characters of new species of shells from the collection formed by Mr. Cuming on the western coast of South America, and among the islands of the South Pacific Ocean. *Proceedings of the Zoological Society of London*. 1833: 16–22.

Takahama, N., Y. Ganzawa, Y. Kamoi, and T. Otsuka. 1976. The Neogene stratigraphy in the northern part of Niigata Prefecture, Japan. *Contributions from the Department of Geology and mineralogy, Niigata University* 4: 97–104. (in Japanese with English abstract)

Tsuda, K. 1965. Neogene molluscan assemblages in the Inner Zone of Northeast Japan -with special reference to the middle Miocene assemblages. *Fossils (Palaeontological Society of Japan)* 10: 20–23. (in Japanese)

Vermeij, G.J. 2013. Molluscan marginalia: Hidden morphological diversity at the bivalve shell edge. *Journal of Molluscan Studies* 79: 283–295.

Watanabe, M. and Y. Yanagisawa. 2005. Refined Early Miocene to Middle Miocene diatom biochronology for the middle- to high-latitude North Pacific. *Island Arc* 14: 91–101.

Yanagisawa, Y. and F. Akiba. 1998. Revised Neogene diatom biostratigraphy for the northwest Pacific around Japan, with an introduction of code numbers for selected diatom biohorizons. *Journal of the Geological Society of Japan* 104: 395–414.

Yanagisawa, Y. and M. Watanabe. 2017. Marine diatom biostratigraphy of the Neogene sequence in the southern part of the Osado Mountain area, Sado Island, Niigata Prefecture, Japan. *Bulletin of the Geological Survey of Japan* 68: 287–339. (in Japanese with English abstract)

Yanai, S., K. Aoki, and Y. Akahori. 2010. Opening of Japan Sea and Major Tectonic Lines of Japan: MTL, TTL and Fossa Magna. *Journal of Geography* 119: 1079–1124. (in Japanese with English abstract)

## RESEARCH NOTE

**Imposex in the city: First evidence of female masculinization in Queen Conch *Aliger gigas* (Linnaeus, 1758) (Gastropoda: Strombidae) in Florida****Justin N. Voss****Gabriel A. Delgado**Fish and Wildlife Research Institute  
Florida Fish and Wildlife Conservation Commission  
Marathon, Florida 33050, USA**Nancy J. Brown-Peterson**Center for Fisheries Research and Development  
School of Ocean Science and Technology  
University of Southern Mississippi  
Ocean Springs, Mississippi 39566, USA**Einat Sandbank****Robert A. Glazer**Fish and Wildlife Research Institute  
Florida Fish and Wildlife Conservation Commission  
Marathon, Florida 33050, USA

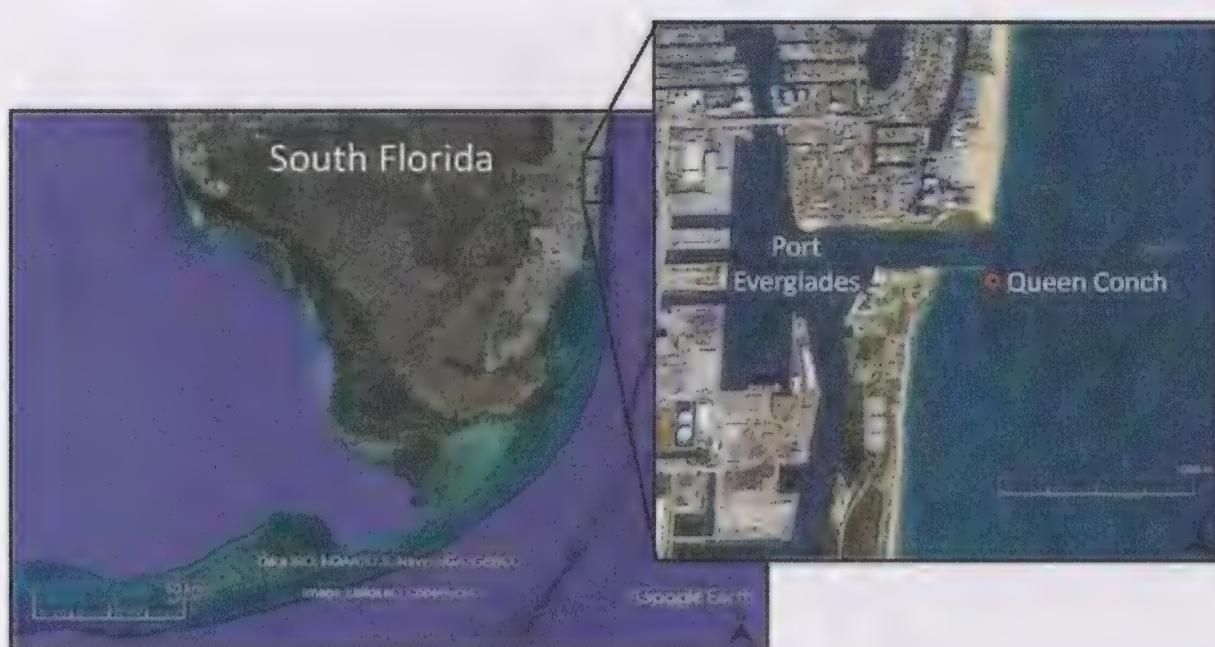
Organotins, such as tributyltin (TBT), are chemical compounds added to antifouling paint that were used worldwide on oceangoing vessels from the 1960s until 2008, when the International Maritime Organization banned them globally through the International Convention on the Control of Harmful Antifouling Systems on Ships (Horiguchi, 2017; Laranjeiro et al., 2018). The use of organotins adversely impacted growth, development, and reproduction in numerous marine organisms (Horiguchi, 2017; Vogt et al., 2018). Despite the global ban, organotins can persist in the environment for decades (Filipkowska et al., 2014; Horiguchi, 2017), thus still posing a threat to susceptible species. In gastropods, organotin exposure can lead to the development of a condition known as imposex (Bryan et al., 1988; Horiguchi, 2017). Imposex is the superimposition of male reproductive tissues (i.e., penis and vas deferens) onto female gastropods and is caused by disruption of the neuroendocrine system (Oberdorster et al., 2005; Horiguchi, 2017). Continued exposure to organotins increases masculinization in females and can reduce fecundity (Averbuj and Penchaszadeh, 2010). In severe cases, the vaginal opening is blocked, resulting in sterility (Bryan et al., 1988; Horiguchi et al., 1995), ultimately leading to large population declines (Cadee et al., 1995; Horiguchi et al., 2006). Imposex in the natural environment is almost exclusively associated with organotin exposure (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017), to the point that imposex in gastropods is used as a biomarker for TBT contamination (Oehlmann et al., 2007; Horiguchi, 2017).

The incidence of gastropod imposex is higher near shipping channels, industrial seaports, and marinas (Li and Collin 2009; Averbuj and Penchaszadeh, 2010; Laranjeiro et al., 2018). The Queen Conch, *Aliger gigas* (Linnaeus, 1758), is a large, gonochoristic marine gastropod that has been protected in Florida since 1986 because of overfishing. A well-documented breeding aggregation of Queen Conch (Berry et al., 2016) sits adjacent to Port Everglades (Figure 1), one of the busiest industrial seaports in the United States (<http://www.porteverglades.net>). And while TBT-induced imposex in areas of elevated boating activity occur in the Caribbean (Titley-O’Neal et al., 2011), imposex has never been reported in Queen Conch in Florida.

We conducted a demographic survey of the Port Everglades Queen Conch aggregation on August 30, 2007, and another on June 27, 2018. A 100-m tape was deployed along one margin of the aggregation; five secondary tapes were then placed perpendicular to the primary tape at random intervals. A secondary tape extended either 100 m into the aggregation or, if positioned at a point at which the aggregation was less than 100 m wide, to its distant margin. Scuba divers counted all adult Queen Conch (defined as having a fully flared lip approximately 10 mm thick or more) within 1 m either side of the secondary tapes to estimate the density of the aggregation. Identifying the sex of a conch *in situ* requires turning it over and patiently waiting for its body to emerge. Because of the time constraints of scuba surveys, individuals were not sexed, but reproductive behaviors (i.e., mating and egg laying) were noted.

Our two aggregation surveys yielded comparable results in terms of density and the percentage of Queen Conch engaged in reproductive behaviors. In 2007, we surveyed 1000 m<sup>2</sup> and counted 73 adult Queen Conch, for a density of 730 ha<sup>-1</sup>. Of these, 5.5% were mating and 9.6% were laying egg masses. During the 2018 survey, we surveyed 850 m<sup>2</sup> and counted 42 adult Queen Conch, for a density of 494 ha<sup>-1</sup>. Of these, 4.8% were mating and 11.9% were laying egg masses.

During the 2018 survey, nine female conchs (so identified because they were mating or egg laying) were collected for assessment of ovarian condition. After removing the bodies from their shells, we observed and recorded that some of these females exhibited imposex (Figure 2). We moved on to collect a sample of ovary tissue from each female, excising a piece of tissue approximately 1 cm<sup>3</sup> from the middle of each ovary. The samples were placed in labeled plastic cassettes and fixed for seven days in 10% neutral buffered formalin. Following fixation, we prepared the ovarian tissues for histological assessment of ovarian maturity and the percentage of developed ovarian tissue using the methods of Delgado et al. (2004). For each female, we also recorded



**Figure 1.** Map of South Florida indicating the location of Port Everglades. Inset shows the site of the Queen Conch aggregation found at the entrance to Port Everglades.

four morphological measurements, as described by Delgado et al. (2019): shell length, lip thickness, shell weight, and body weight. Unpaired t-tests, performed in Sigma Plot 13 (Systat Software Inc., San Jose, CA, USA), were used to test for differences in histology and morphology between females exhibiting imposex and normal females. Results were considered statistically significant if  $P < 0.05$ .

For each female, we ranked the severity of imposex using the scale developed by Cob et al. (2011), which ranges from 0 (i.e., normal; no imposex) to 3 (i.e., having a complete penis). Imposex was observed in four of the nine females (44.4%). One female was characterized as having stage-1 imposex (Figure 2). The other three females were characterized as having stage-2 imposex (Figure 2). From histology, all four females with imposex were classified as ripe and spawning-capable (i.e., they had tertiary vitellogenic oocytes, with oocytes in the oviduct; Figure 3). Imposex-affected and normal females did not differ significantly in shell length ( $t = -1.514$ ;  $df = 7$ ;  $P = 0.174$ ),

lip thickness ( $t = 0.037$ ;  $df = 7$ ;  $P = 0.972$ ), shell weight ( $t = 1.275$ ;  $df = 7$ ;  $P = 0.243$ ), body weight ( $t = -1.976$ ;  $df = 7$ ;  $P = 0.089$ ), or the percentage of developed ovarian tissue ( $t = 1.331$ ;  $df = 7$ ;  $P = 0.225$ ) (Table 1).

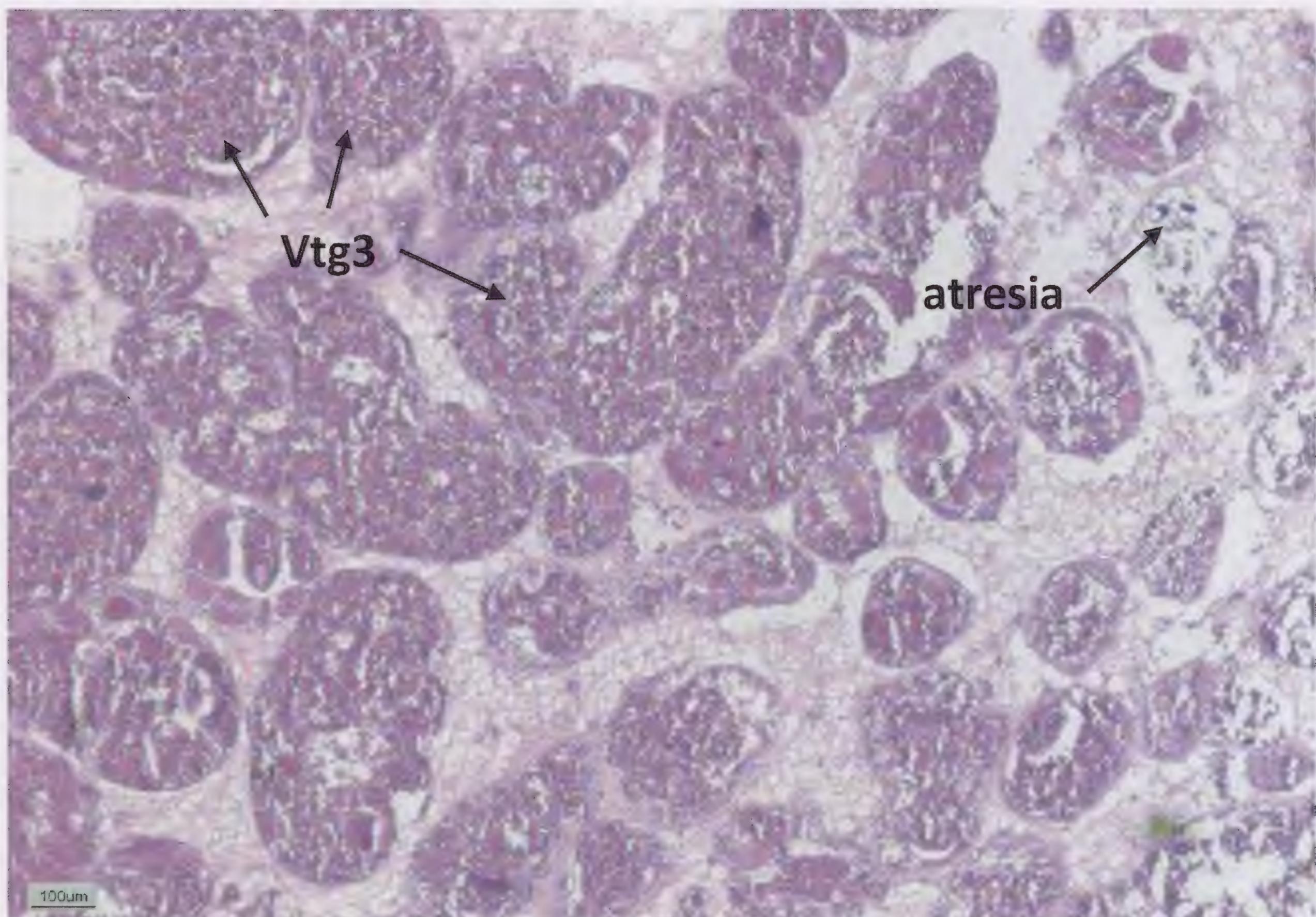
This is the first documented case of imposex in Queen Conch in Florida. While we did not test for the presence of organotins at the aggregation site, the proximity to a major shipping port suggests that organotin exposure was the likely cause of the malady (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017). The marine habitats surrounding Port Everglades are almost certainly contaminated with organotins that predate the antifoulant ban in 2008 as evident by the fact that the nearby disposal site for dredged material from Port Everglades is heavily contaminated by organotins (U.S. EPA and USACE 2020). Although organotin is banned from being sold in 67 countries, it is still manufactured and sold in many Caribbean and South American countries (Turner and Glegg, 2014). Ships originating from these countries may be a more recent source of contamination.

There may be other endocrine disruptors that might be causing imposex at Port Everglades, but the overwhelming evidence from the literature suggests organotin exposure (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017). That said, the extent of organotin contamination around South Florida is unknown. Future research should include water, sediment, and tissue assays to determine the extent of organotin contamination around South Florida and could also include a local member of the widespread *Stramonita haemastoma* (Linnaeus, 1767) species complex such as *Stramonita floridana* (Conrad, 1837) to serve as a bioindicator (*sensu* Stickle and Zhang, 2003; Limaverde et al., 2007).

In contrast to studies finding that imposex negatively affects reproduction in gastropods (Horiguchi et al., 2006; Lahbib et al., 2009; Averbuj and Penchaszadeh, 2010),



**Figures 2.** Two imposex-affected female Queen Conch from Port Everglades, Florida (removed from shells).



**Figure 3.** Histological section of ovarian tissue from an imposex-affected Queen Conch from Port Everglades, Florida. This female was classified as ripe and spawning-capable. Note the abundant tertiary vitellogenic oocytes (Vtg3) throughout the ovarian tissue; minor atresia (i.e., resorption of some vitellogenic oocytes) can also be seen.

the >40% incidence rate of imposex in our samples did not seem to affect reproductive activities. The percentage of Queen Conch mating and laying eggs in the Port Everglades aggregation was similar to that reported elsewhere in Florida (Delgado and Glazer, 2020), where no imposex has been reported (Delgado et al., 2004, 2019). Based on histology, the ovaries of the females afflicted with imposex were indistinguishable from those of normal, ripe females. This may be because, while the incidence rate of imposex was relatively high, the severity of the affliction was not in the advanced stages. The

**Table 1.** Morphological and histological measurements (mean  $\pm$  1 standard error) of female Queen Conch from Port Everglades, Florida.

	Imposex-affected	Normal
Shell length (cm)	$22.5 \pm 0.62$	$23.8 \pm 0.58$
Lip thickness (mm)	$28.3 \pm 2.01$	$28.2 \pm 1.32$
Shell weight (g)	$2,615 \pm 161$	$2,338 \pm 146$
Body weight (g)	$355 \pm 29.6$	$474 \pm 47.9$
Ovarian tissue (%)	$97.0 \pm 1.92$	$92.8 \pm 2.35$

females we examined were engaged in reproductive activities, which may have biased our results; there may be females within the aggregation with more severe cases of imposex that are not reproductively active. Future research might explore the relationship between age and imposex severity and incidence rate, because older females will have been exposed longer.

Studies of imposex in other strombids have reported morphological differences between imposex-affected and normal females. In *Strombus pugilis* Linnaeus, 1758 and *Conomurex luhuanus* (Linnaeus, 1758), imposex-affected females were larger and heavier than normal females (Reed, 1993, 1995). In *Laevistrombus canarium* (Linnaeus, 1758), imposex-affected females had larger and heavier shells but lighter bodies than did normal females (Cob et al., 2008). However, we did not observe statistically significant differences in gross morphology between imposex-affected and normal females. This may have been because of the comparatively mild severity of imposex in the females we examined.

Imposex can cause population declines in gastropods (Cadee et al., 1995; Horiguchi et al., 2006), but this was not observed in Queen Conch at Port Everglades. The

demographics of the aggregation remained steady over our two surveys and were consistent with those reported by Berry et al. (2016). Berry et al. (2016), however, noted abnormal egg masses at the Port Everglades aggregation. Normal egg masses are crescent shaped and covered with sand; the abnormal ones were stringy and not covered with sand (Berry et al., 2016: fig 7). We also observed females laying abnormal egg masses. In other gastropods, egg laying becomes disrupted in advanced stages of imposex (Horiguchi, 2017), which may explain why some Queen Conch females at Port Everglades lay abnormal egg masses, but further study is needed.

It is unknown whether the offspring of imposex-affected females are as viable as those from normal Queen Conch. Other pollutants can cause transgenerational effects in mollusks that reduce larval growth and survival (Nice et al., 2003) and juvenile fitness (Osborne et al., 2020). If the veligers and juveniles from imposex-affected Queen Conch are compromised, this may have negative consequences for larval connectivity to downstream populations and metapopulation persistence.

Beyond the effects on Queen Conch, the results from this study highlight the deleterious impacts that society may have on wildlife resources that are juxtaposed closely to urban centers. Organotins represent only one in a much wider suite of chemicals that enter the South Florida nearshore marine environment from sources as diverse as agriculture (e.g., fertilizers, herbicides, pesticides), industry, recreation (e.g., golf course fertilization and pesticide application), and residential activities (e.g., sewage). How society values these resources and prioritizes the mitigation of the pernicious threats associated with point and non-point sources of pollution will ultimately determine the overall health of nearshore ecosystems and the sustainability of the resources they support.

## LITERATURE CITED

Averbuj, A. and P.E. Penchaszadeh. 2010. On the reproductive biology and impact of imposex in a population of *Buccinanops monilifer* from Mar del Plata, Argentina. Journal of the Marine Biological Association of the United Kingdom 90: 729–734.

Berry, C., R.L. Hill, and B.K. Walker. 2016. Demographics of a nearshore mating queen conch (*Lobatus gigas*) aggregation on the southeast Florida Reef Tract. Bulletin of Marine Science 92: 59–73.

Bryan, G.W., P.E. Gibbs, and G.R. Burt. 1988. A comparison of the effectiveness of tri-n-butyltin chloride and five other organotin compounds in promoting the development of imposex in the dogwhelk, *Nucella lapillus*. Journal of the Marine Biological Association of the United Kingdom 68: 733–744.

Cadee, G.C., J.P. Boon, C.V. Fischer, B.P. Mensink, and C.C. Ten Hallers-Tjabbes. 1995. Why the whelk (*Buccinum undatum*) has become extinct in the Dutch Wadden Sea. Netherlands Journal of Sea Research 34: 337–339.

Cob, Z.C., A. Arshad, J.S. Bujang, and M.A. Ghaffar. 2011. Description and evaluation of imposex in *Strombus canarium* Linnaeus, 1758 (Gastropoda, Strombidae): A potential bio-indicator of tributyltin pollution. Environmental Monitoring and Assessment 178: 393–400.

Cob, Z.C., A. Arshad, M.H. Idris, J.S. Bujang, and M.A. Ghaffar. 2008. Sexual polymorphism in a population of *Strombus canarium* Linnaeus, 1758 (Mollusca: Gastropoda) at Merambong Shoal, Malaysia. Zoological Studies 47: 318–325.

Delgado, G.A., C.T. Bartels, R.A. Glazer, N.J. Brown-Peterson, and K.J. McCarthy. 2004. Translocation as a strategy to rehabilitate the queen conch (*Strombus gigas*) population in the Florida Keys. Fishery Bulletin 102: 278–288.

Delgado, G.A. and R.A. Glazer. 2020. Demographics influence reproductive output in queen conch (*Lobatus gigas*): implications for fisheries management. Bulletin of Marine Science 96: 707–721.

Delgado, G.A., R.A. Glazer, and N.J. Brown-Peterson. 2019. Arrested sexual development in queen conch (*Lobatus gigas*) linked to abnormalities in the cerebral ganglia. Biological Bulletin 237: 241–249.

Filipkowska, A., G. Kowalewska, and B. Pavoni. 2014. Organotin compounds in surface sediments of the Southern Baltic coastal zone: A study on the main factors for their accumulation and degradation. Environmental Science and Pollution Research 21: 2077–2087.

Horiguchi, T. 2017. Biological Effects by Organotins. Springer, Tokyo, Japan. 254 pp.

Horiguchi, T., M. Kojima, F. Hamada, A. Kajikawa, H. Shiraishi, M. Morita, and M. Shimizu. 2006. Impact of tributyltin and triphenyltin on ivory shell (*Babylonia japonica*) populations. Environmental Health Perspectives 114: 13–19.

Horiguchi, T., H. Shiraishi, M. Shimizu, S. Yamazaki, and M. Morita. 1995. Imposex in Japanese gastropods (Neogastropoda and Mesogastropoda): Effects of tributyltin and triphenyltin from antifouling paints. Marine Pollution Bulletin 31: 402–405.

Lahbib, Y., S. Abidli, and N.T. El Menif. 2009. Relative growth and reproduction in Tunisian populations of *Hexaplex trunculus* with contrasting imposex levels. Journal of Shellfish Research 28: 891–898.

Laranjeiro, F., P. Sánchez-Marín, I.B. Oliveira, S. Galante-Oliveira, and C. Barroso. 2018. Fifteen years of imposex and tributyltin pollution monitoring along the Portuguese coast. Environmental Pollution 232: 411–421.

Li, C. and R. Collin. 2009. Imposex in one of the world's busiest shipping zones. Proceedings of the Smithsonian Marine Science Symposium 1: 189–196.

Limaverde, A.M., A. de L. Rebello Wagener, M. A. Fernandez, A. de L. Scofield, and R. Coutinho. 2007. *Stramonita haemastoma* as a bioindicator for organotin contamination in coastal environments. Marine Environmental Research 64: 384–398.

Nice, H.E., D. Morritt, M. Crane, and M. Thorndyke. 2003. Long-term and transgenerational effects of nonylphenol exposure at a key stage in the development of *Crassostrea gigas*. Possible endocrine disruption? Marine Ecology Progress Series 256: 293–300.

Oberdorster, E., J. Romano, and P. McClellan-Green. 2005. The neuropeptide APGWamide as a penis morphogenic factor (PMF) in gastropod mollusks. Integrative and Comparative Biology 45: 28–32.

Oehlmann, J., P. Di Benedetto, M. Tillmann, M. Duft, M. Oetken, and U. Schulte-Oehlmann. 2007. Endocrine disruption in prosobranch molluscs: Evidence and ecological relevance. Ecotoxicology 16: 29–43.

Osborne, R.K., P.L. Gillis, and R.S. Prosser. 2020. Transgenerational effects of copper on a freshwater gastropod,

*Planorbella pilsbryi*. Freshwater Mollusk Biology and Conservation 23: 42–54.

Reed, S.E. 1993. Size differences between sexes (including masculinized females) in *Strombus pugilis* (Mesogastropoda: Strombidae). Journal of Shellfish Research 12: 77–79.

Reed, S.E. 1995. Sexual trimorphism in *Strombus luhuanus*, Linne 1758 (Mollusca: Gastropoda) at Shirahama, Japan. Journal of Shellfish Research 14: 159–160.

Sternberg, R.M., M.P. Gooding, A.K. Hotchkiss, and G.A. LeBlanc. 2010. Environmental-endocrine control of reproductive maturation in gastropods: Implications for the mechanism of tributyltin-induced imposex in prosobranchs. Ecotoxicology 19: 4–23.

Stickle, W.B. and Z. Zhang. 2003. Long-term trends in imposex in six populations of *Stramonita haemastoma*. Bulletin of Marine Science 72: 685–694.

Titley-O'Neal, C.P., B.A. MacDonald, E. Pelletier, R. Saint-Louis, and O.S. Phillip. 2011. The relationship between imposex and tributyltin (TBT) concentration in *Strombus gigas* from the British Virgin Islands. Bulletin of Marine Science 87: 421–435.

Turner, A. and G. Glegg. 2014. TBT-based antifouling paints remain on sale. Marine Pollution Bulletin 88: 398–400.

U.S. Environmental Protection Agency (U.S. EPA), and U.S. Army Corps of Engineers (USACE), Jacksonville District. 2020. Draft environmental assessment on the expansion of the Port Everglades harbor ocean dredge material disposal site (ODMDS). Broward County, Florida. February 2020. 130.

Vogt, É.L., J.F.A. Model, and A.S. Vinagre. 2018. Effects of organotins on crustaceans: Update and perspectives. Frontiers in Endocrinology 9: 65.

## AUTHOR INDEX

AMANO, K. ....	51, 132	MODYS, A.B. ....	36
ASOREY, C.M. ....	61	OLEINIK, A.E. ....	36
BERTSCH, H. ....	71	OLIVEIRA, C.D.C. ....	57
BIELER, R. ....	61	POWELL II, C.L. ....	107
BROWN-PETERSON, NANCY J. ....	138	SANDBANK, E. ....	89
COSTA, P.M.S. ....	95	SELLANES, J. ....	61
CUCCINELLO, S.E. ....	92	SHARP, W.C. ....	89
DELGADO, G.A. ....	89, 138	SMITH, M.L. ....	1
EASTON, E.E. ....	61	SNEDDON, D.J. ....	1
GOMES, R.S. ....	95	SOUZA, L.S. ....	95
GUTIERREZ-ANDRADE, D. ....	92	TETU, A.M. ....	36
HOUART, R. ....	117	VOSS, J.N. ....	138
KURITA, H. ....	132	WATTERS, G.T. ....	1
LIMA, T.C. ....	57	WIEDRICK, S.G. ....	117
MEADE, K.J. ....	107	ZHANG, SH. ....	45
MECHO, A. ....	61	ZHANG, SU. ....	45
MIDDLEBROOKS, M. ....	92		

## NEW TAXA PROPOSED IN VOLUME 134

### GASTROPODA

<i>Bathyacmaea austrina</i> S.-Q. Zhang and S.-P. Zhang, 2020, new species (Pectinodontidae) ....	46
<i>Bathyacmaea brevidentata</i> S.-Q. Zhang and S.-P. Zhang, 2020, new species (Pectinodontidae) ....	48
<i>Paciocenebrina bormannae</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	118
<i>Paciocenebrina grandilurida</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	120
<i>Paciocenebrina mininterfossa</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	121
<i>Paciocenebrina murphyorum</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	124
<i>Paciocenebrina pseudopusilla</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	124
<i>Paciocenebrina pusilla</i> Wiedrick and Houart, 2020, new species (Muricidae) ....	126
<i>Rolleia simonaikeni</i> Watters, Smith, and Sneddon, 2020, new species (Annulariidae) ....	30
<i>Tritonoharpa curvapex</i> Souza, Gomes, and Costa, 2020, new species (Cancellariidae) ....	96

### BIVALVIA

<i>Arca (Arca) budoensis</i> Amano, 2020, new species (Arcidae, fossil) ....	124
<i>Cuspidaria inouei</i> Amano and Kurita, 2020, new species (Cuspidariidae, fossil) ....	53

## REVIEWERS FOR VOLUME 134

Beck, Lothar	Harasewych, M.G.	Pearce, Timothy A.
Behrens, David	Jenkins, Robert G.	Portell, Roger W.
Bieler, Rüdiger	Kantor, Yuri	Rosenberg, Gary
Bogan, Arthur E.	Kiel, Steffen	Ter Poorten, Jan Johan
Breure, Abraham	Lee, Harry G.	Slapcinsky, John
Coan, Eugene V.	Lutaenko, Konstantin A.	Stanley, Richard G.
Davis, Megan	McGann, Mary L.	Stout, Carla
Fallon, Philip	Nielsen, Sven	Valentich-Scott, Paul
Flint, Mark	Oberdoster, Eva	Verhecken, André
Frost, Thomas P.	Oliver, Graham	Walker, Brian
Garrigues, Bernard	Orstan, Aydin	Zelaya, Diego
Groves, Lindsey		

Sponsored in part by the State of  
Florida, Department of State,  
Division of Cultural Affairs and the  
Florida Council on Arts and Culture



## INSTRUCTIONS TO AUTHORS

---

*The Nautilus* publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as Research Notes and do not require an abstract.

**Manuscripts:** Each original manuscript and accompanying illustrations should be submitted to the editor via e-mail. Authors should follow the general recommendations of Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers, available from the Council of Science Editors at <http://www.scientificstyleandformat.org/Home.html>.

The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. The sequence of sections should be Title, Author(s) and Affiliations, Abstract, Additional Keywords, Introduction, Materials and Methods, Results, Discussion, Conclusions, Acknowledgments, Literature Cited, Tables, Figure Captions, Figures. If the author for correspondence is not the senior author, please indicate in a footnote. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional keywords. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of *The Nautilus* for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

**Illustrations:** Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). “Tall” page-width illustrations should be avoided, square or “landscape” formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual (printed) size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . ., NOT Figures 1A, 1B, 1C, . . ., NOR Plate 1, Figure 1, . . .). In illustrations with more than one figure, make sure that blank areas between figures should be kept to a minimum, thereby allowing for more area for each individual figure.

Compressed (e.g., .jpg) or other low-resolution file formats may be used to facilitate original submission and the review process, but may not be acceptable at final submission (see below).

**Types and Voucher Specimens:** Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly recommended, as is the deposition of representative voucher specimens for all other types of research work.

**The Editorial Process:** Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are sub-standard or not appropriate in scope for journal. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers' comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

**Final Submission:** Authors of accepted manuscripts are required to submit a final version to the editor at [jleal@shellmuseum.org](mailto:jleal@shellmuseum.org). High-resolution image files may be sent to the editor at this stage.

**Proofs:** After typesetting, proofs will be sent to the author. Author should read proofs carefully and send corrections to the editor within 48 hours. Changes other than typesetting errors will be charged to the author at cost.

**Offprints:** An order form for offprints will accompany the proofs. Offprints will be ordered directly from the editor. Authors with institutional, grant, or other research support will be asked to pay for page charges at the rate of \$60 per page.

More information at <http://shellmuseum.org/learn/the-nautilus>.

SMITHSONIAN LIBRARIES



3 9088 01972 9557